

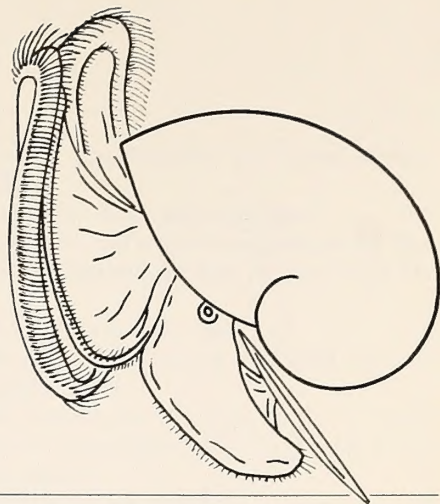




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THE VELIGER

A Quarterly published by
CALIFORNIA MALACOOLOGICAL SOCIETY, INC.
Berkeley, California
R. Stohler, Founding Editor



Volume 26

July 1, 1983 to April 2, 1984

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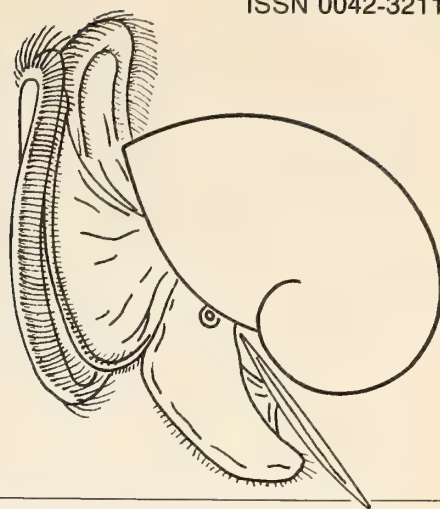
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THE VELIGER

Scope of the journal

The Veliger is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater, or terrestrial mollusks from any region will be considered. Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimen must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Very short papers, generally not exceeding 500 words, will be published in a column entitled "NOTES, INFORMATION & NEWS"; in this column will also appear notices of meetings, as well as news items that are deemed of interest to our subscribers in general.

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Send manuscripts, proofs, books for review, and correspondence regarding editorial matters to: David W. Phillips, Editor, 2410 Oakenshield Road, Davis, CA 95616 USA.

TO OUR READERS

The previous issue, Volume 25, Number 4, marked the completion of 25 years of growth and success of *The Veliger*, success due in great measure to the efforts of one man, Rudolf Stohler. The climb is by no means over. With Volume 26, Number 1, we begin again, advancing by standing on the shoulders of our predecessors.

Some changes in format and style will be apparent to readers of the current issue. Our journal is now being produced by Allen Press, a quality commercial printing house specializing in scholarly journals and books. And there is a new Editor. Prospective authors may wish to consult the revised "Instructions to Authors" printed on the inside back cover. There are some changes.

Despite these changes, our purpose remains the same. The California Malacozoological Society, through its journal *The Veliger*, remains committed to disseminating new information in the field of malacology and conchology as widely as possible at the lowest cost possible. We likewise reaffirm our continuing commitment to meeting ever higher standards for the publication of scientific information.

There is no reason why *The Veliger* should not continue to grow for another 25 years. Our Society is vigorous and healthy. However, ominously escalating costs of publication have already threatened many a once healthy society. The simple truth is that we will need increased levels of income to balance our increased production costs. Readers can help ensure the continued publication of *The Veliger* by joining the Society (or by renewing their membership) and by encouraging their local and University libraries to subscribe. Donations are, of course, another extremely important means of ensuring the success of our Society (contributions to CMS are tax deductible).

A new beginning is a time to reaffirm our purpose, to acknowledge the many splendid contributions that have brought us this far, and to seek ways to improve. The new Editor asks you to support the Society and invites the comments of readers, members, and prospective authors. He looks forward to serving you.

D. W. Phillips, Editor



Photograph by Leroy Poorman.

RUDOLF STOHLER

OUR THANKS TO RUDOLF STOHLER

With the completion of Volume 25 of *The Veliger*, Dr. Stohler has retired as Editor—stepping aside for some well-earned rest while still able to help us with his counsel and to inspire us with his unabated interest and enthusiasm. It is a good time to look back over the history of *The Veliger*, and to reflect gratefully how much we owe to the efforts of one devoted individual.

To many who have read and contributed to *The Veliger*, Rudolf Stohler may be simply an exacting Editor, a stickler for accuracy and good order in writing; to those of us who from time to time have transgressed, he is one who can communicate in pithy language; to those of us who have appealed for help, he has been ready with advice and assistance. But Rudolf has done much more than found and edit *The Veliger*, and we should fill in the picture of his pre-*Veliger* years, for information on which we are indebted to Professor Emeritus Richard Eakin, long-time Chairman of the Department of Zoology at the University of California, Berkeley.

Rudolf Stohler earned his Ph.D. at the University of Basel in his native Switzerland, and in the period of 1926–1932 published a series of papers on the chromosomes of European toads and their ovaries and Bidder's organs. He came to California in 1928 as a Rockefeller Fellow to work with Dr. K. F. Meyer at the Hooper Foundation on the University of California's San Francisco campus. The first day, as he arrived at the laboratory early, as was and is his habit, he picked up a large beetle that aroused his zoological curiosity. A young lady coming to work offered to obtain a bottle for the specimen. The Fellow was impressed with her kindness and friendliness and decided, then and there, that he wanted her for his wife. A year later Genevieve and Rudolf were married.

Dr. Stohler had expected to continue his study of sex determination and differentiation in amphibians, but Professor Meyer had other plans for him, namely, that he work as an assistant on paralytic shellfish poisoning. At first it appeared that diatoms, found in abundance by Stohler in the guts of mussels and clams, might be the source of the lethal poison. Without more evidence Professor Meyer immediately published a paper, as sole author, to that effect. Later, Dr. Stohler disproved that hypothesis. The source of the toxin was found to be *Gonyaulax* or other red tide flagellates that are eaten by the bivalves.

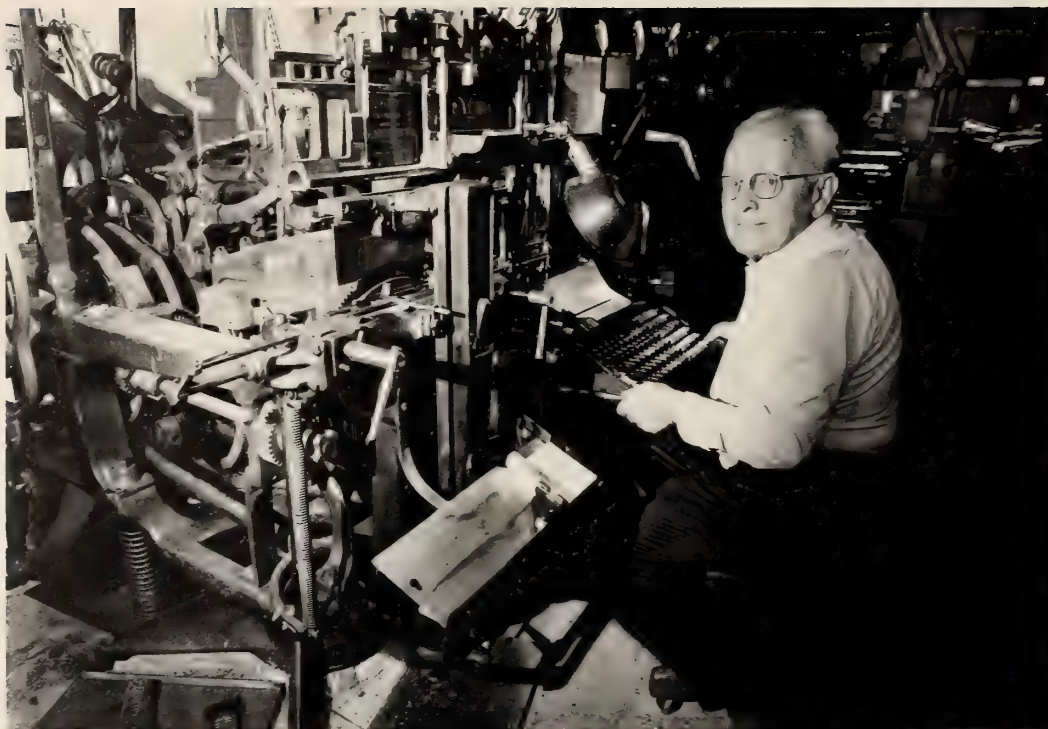
After the completion of the fellowship, the Stohlers emigrated to Switzerland, but as the climate was unsuitable for the young bride the couple returned to Berkeley in 1932. Dr. Stohler was appointed a Research Associate (an honorary title but without salary) by Professor C. A. Kofoed, then Chairman of the Department of Zoology, University of California, Berkeley. Again Dr. Stohler was not free to pursue his own research because he was assigned to projects of Kofoed's. To earn a living Stohler organized classes in German. Among his students were Alden Miller, later a Director of the Museum of Vertebrate Zoology, and Richard Eakin, later a Chairman of Zoology. In 1941 he was appointed to the position of Specimen Preparator and Collector for the Department of Zoology. In these capacities he ranged the California coast collecting for classes and for research, and developing a wide circle of friends and scientific colleagues. Later, under the Chairmanship of Richard Eakin, Dr. Stohler was relieved of some of his service responsibilities by appointment as a Research Zoologist (the research equivalent of a professorship) and was given an assistant and time to devote to his malacological interests.

Dr. Stohler has also had a career of teaching. In 1934 he gave the departmental courses in cytology and assisted Professor Kofoed in courses in protozoology and parasitology while Professor Harold Kirby was on sabbatical leave. For many years he gave courses in the University of California Extension Division in Oakland, San Francisco, and Berkeley. And he has generously advised graduate students and faculty on procurement of research material, on nomenclatural and taxonomic problems, and on scientific writing.

In the early 1950's Rudolf Stohler and several colleagues of like interests founded the Northern California Malacozoological Club, the rather imposing name reflecting that the group was broadly interested in molluscan biology and not merely in "shell-collecting." On June 27, 1958, appeared a mimeographed Club newsletter, "*The Veliger*," suitably named for an infant mollusc.

The new publication grew rapidly and by its fourth year contained 220 pages and had appeared in printed format—made possible because Stohler had, out of his own pocket, acquired and set up in his basement an old linotype machine. Over twenty years later, on this machine, now supplied with a dozen different type-faces, Stohler still regularly set type for *The Veliger*, which since 1967 has run to over 400 pages annually.

After many years' investment of Stohler's skill and labor, not to mention over \$7,000 of his own money, *The Veliger* had clearly outgrown the needs of the Club and was incorporated by a small support group, the California Malacozoological Society, as a non-profit corporation. Stohler, with only a part-time business assistant and the help of various



Photograph by Jane Scherr; courtesy of "California Monthly."

individuals (notably Mrs. Jean Cate), carried on all the essential functions of editing, printing, and distributing the journal, whose circulation is now over 800.

The corporation undertook to repay Stohler his \$7,000 investment. But, in setting up the corporation, Stohler had instituted an endowment fund, the capital of which cannot be touched, but the income from which can be used to help support publication, for example, of papers with expensive illustrations that cost more than an author can afford. As fast as the corporation paid back installments on the debt, Stohler put the money into the Endowment Fund, to aid the publication (contributions to this fund have come from many friends and are, of course, still enthusiastically welcomed).

The success of *The Veliger*, which has never received a penny of foundation support, is a remarkable example, in this day of heavily-funded, group-supported ventures, of what one person with skill, energy, and devotion can accomplish. The first 25 volumes of *The Veliger* form a fitting and living monument, and it is our hope and intention that Rudolf will see it flourish for many years to come.

To characterize Rudolf Stohler as a person is not easy. Even more solid than *The Veliger*, Rudolf radiates energy and enthusiasm. Generally at the Zoology Department well before anyone else, Rudolf moves with a brisk, perhaps bouncy, style. Extremely helpful to those needing and seeking his help, and sympathetic to personal needs of students, Rudolf is yet one who does not suffer fools gladly. Above all, he detests sloppiness in anything, physical or mental. His choicest comments have been reserved for his favorite *bête noir*, the U.S. Postal Service, but others have not escaped. Yet all who have known Rudolf know that behind the sometimes pungent manner there lies a deep decency, integrity, kindness, and high personal standards. Rudolf has not lightly retired as Editor of *The Veliger*, and doubtless feels like many a parent watching his child venture out into the world. His principal concern is that *The Veliger* maintain high standards. To this aim the Executive Committee of the California Malacozoological Society and the new Editor are committed.

A final word needs to be said. In all his work for over 50 years Rudolf has had the support of his devoted wife, Genevieve, who has shared heavily in the labor and frustrations of producing *The Veliger*. Although inconspicuous in the background, she has nevertheless earned our deepest gratitude.

R. I. Smith

New Molluscan Species (Gastropoda: Neogastropoda) from the Tropical Eastern Pacific

by

LEROY H. POORMAN

15300 Magnolia Street, Space 55, Westminster, California 92683

Abstract. Three new species are described: *Murexiella venustula* Poorman, spec. nov., off the southern coast of Isla Santa Cruz, Galápagos Islands, Ecuador, and probably the Gulf of California; *Daphnella levicallis* Poorman, spec. nov., off Estero San Carlos, Sonora, Mexico; *Anachis* (*Parvanachis*) *mullineri* Poorman, spec. nov., in Bahía de Santiago, Colima, Mexico.

TWENTY-NINE YEARS of observing and collecting mollusks along the west coasts of the Americas has resulted in the recognition of a number of new species, eight of which have already been published. Three additional species are described herein.

Murexiella Clench & Pérez Farfante, 1945

Type species: *Murex hidalgoi* Crosse, 1869, by original designation.

The small, stoutly fusiform shell has four or more varices with foliated spines connected by a laminated webbing. The siphonal canal is moderately broad and extended. The operculum is muricoid, with a sub-apical nucleus.

Murexiella venustula Poorman, spec. nov.

(Figures 1, 2, 5)

Description: The shell is small and solid, consisting of five whorls and a turbinate protoconch of three turns. Axial sculpture is of seven strong, broad varices per whorl with narrow interspaces. Each varix crosses the shoulder area to the preceding whorl as a thin lamella but is not joined to it. The first several varices of the teleoconch cross the lower half of the last turn of the protoconch and are attached to it. Spiral sculpture on the body whorl is of five broadly flattened, strong cords that are made up of five scabrous threads. There are two cords on each whorl of the spire. All interspaces are narrow, wider at the bottom. At the base of the aperture is one minor cord and there are two strong, flattened cords on the canal. Anterior cords are hollow at their terminations and scarcely reflected as short, stout spines at the crests of the varices. The degree of reflection increases posteriorly along the varix. The

cord at the shoulder is the heaviest and terminates as a large, reflected spine that is twisted toward the apex. There is a major, reflected, open spine at the center of the lamella on the shoulder and a much smaller one near the suture. Areas on the shoulder between the lamellae are flat and show only traces of the two cords causing the spines. The aperture is oval with a nearly complete peristome except along the parietal wall. A shallow, anal sulcus is apparent. Strong crenulations are along the erect outer lip. The spines behind the lip are roundly recurved and are joined for about half their lengths by intricate lamination. The anterior canal is broad and moderately long, nearly straight, narrowly open to the right, and with the end distally recurved. The top and left side of the canal each show four strong, longitudinal threads. Shell color is pinkish beige, with brown on the third spiral cord at the crests of the varices.

Type locality: Off the southern coast of Isla Santa Cruz, Galápagos Islands, Ecuador; 0°47'S Latitude, 90°21'W Longitude; four specimens dredged in 150-200 m.

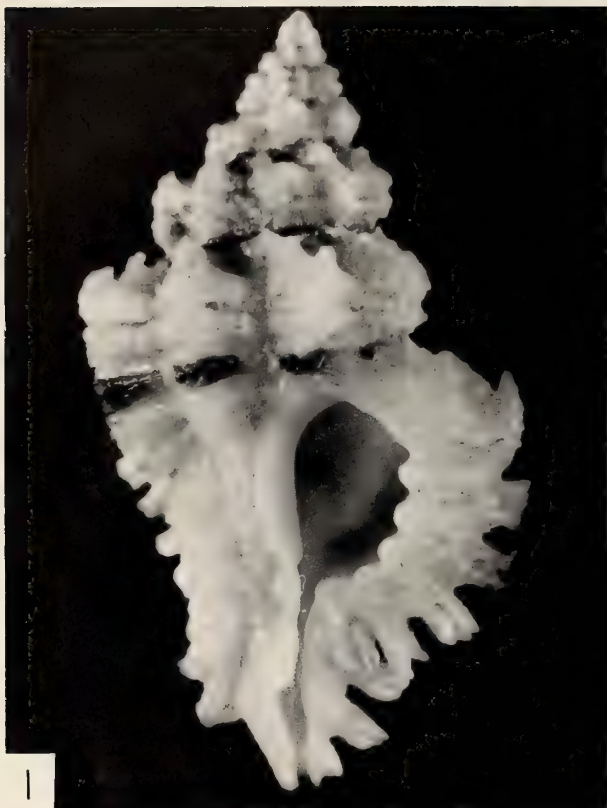
Holotype: San Diego Natural History Museum, SDNHM 81610.

Dimensions of the holotype: Height 19.6 mm, maximum diameter 11.4 mm.

Paratypes: Two paratypes are in the Carl and Laura Shy Collection, Seal Beach, California; one paratype is in the Rose Burch Collection, Seal Beach, California.

One additional specimen was brought in by a fishing boat to Guaymas, Sonora, Mexico, in 1968, probably extending the range to the Gulf of California.

The specific name is taken from the Latin adjective meaning "pretty" or "charming little."



Discussion: This new species is closest to *Murexiella mildredae* Poorman, 1980, in general appearance and in the low, broad, spiral cords overhanging the narrow interspaces (POORMAN, 1980b). It differs in having two, not three, spiral cords on each whorl of the spire, in having numerous and broadly rounded varices, in coloring, and in other sculptural details.

Murexiella venustula, spec. nov., also has a superficial resemblance to *Murexiella laurae* Vokes, 1970. However, the latter species has a different spine structure and has four varices per whorl (only three on some specimens) on the adult shell (POORMAN, 1980a). Also, the general coloring of the two species is completely different.

Hollow spines formed when the leading edges completely circle to touch are not unusual in *Murexiella*. All three of the above species are of this type. Comparison was made with a specimen of *Murexiella mactanensis* Emerson & D'Attilio, 1979, from Bohol Strait, Philippine Islands. Although the shells differ in general appearance, the basic spine structure is similar.

Daphnella Hinds, 1844

Type species: *Pleurotoma lymneiformis* Kiener, 1839–1840.

The shell is cylindro-ovate, slowly contracted to a short, open, truncated, anterior canal. The body whorl is usually more than one-half the shell height. The protoconch is reticulated and of three to four turns. The sinus is sutural, reversed L-shaped. Spiral sculpture is of fine threads over-riding numerous fine, axial ribs. There is no operculum. The shell is irregularly maculated with brown.

Daphnella levicallis Poorman, spec. nov.

(Figures 3, 6)

Description: The shell is larger and more inflated than most species in the genus. The protoconch (eroded on the holotype) is of four turns, narrowly turbinate and diagonally reticulated by fine threads, with small beads at the intersections. The first turn of the protoconch is minute and has small beads (at 250×) arranged in spiral rows and diagonal lines which, by the second turn, become diagonal threads. The last half turn of the protoconch develops a slight, peripheral angulation with the reticulations above the angulation sagging into a band and becoming the trace of the anal sulcus on the teleoconch. The angulation becomes a cord that develops into two

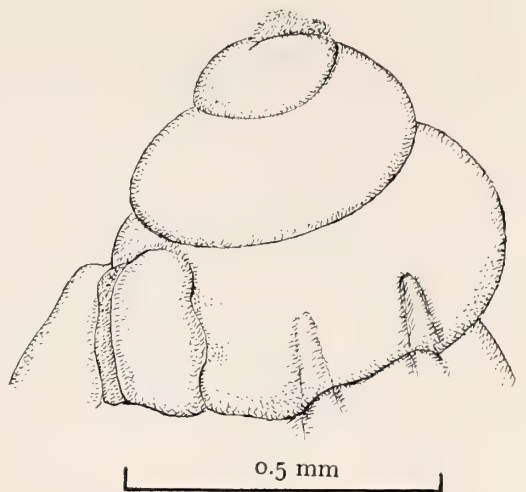


Figure 5

Protoconch of *Murexiella venustula* Poorman, spec. nov. × 80.

threads. These develop into the spiral cords on the teleoconch. The protoconch terminates abruptly in a sinuosity advancing anteriorly. The teleoconch is of six rounded whorls constricted at the suture. Spiral sculpture is of strong threads throughout, 2 on the first turn and 25 on the body whorl. The trace of the anal sulcus is wide and flat, unornamented except for obscure fine threads. Axial sculpture is of numerous low rounded ribs, 10 on the first turn and 25 on the body whorl, extending to the anterior canal. Ribs are crossed by spiral threads in prominent nodes, strongest at the shoulder. The aperture is oval, with a deep J-shaped anal sulcus at the suture. The pillar is nearly straight anteriorly and has light callus. The outer lip is flaring but not produced forward, with a pronounced sinuosity at the lower part. A short, truncated, open, anterior canal is differentiated from the aperture by an angulation in the lip. The outer lip is reinforced by a low ridge of callus just inside, thickest at the anal sinus and at the anterior part of the aperture. Shell color is pale brown maculated with red-brown except for an unmaculated band below the periphery. The third spiral cord below the shoulder is white on early whorls.

Type locality: Five km south of Tetas de Cabra, Estero San Carlos, Sonora, Mexico; 27°54'N Latitude, 111°05'W Longitude; 16 specimens dredged in 80–100 m on broken shell, small rocks, and silt bottom.

Explanation of Figures 1 to 4

Figure 1. Holotype of *Murexiella venustula* Poorman, spec. nov. × 5.6.

Figure 2. Holotype of *Murexiella venustula* Poorman, spec. nov. × 5.6.

Figure 3. Holotype of *Daphnella levicallis* Poorman, spec. nov. × 6.0.

Figure 4. Holotype of *Anachis* (*Parvanachis*) *mullineri* Poorman, spec. nov. × 22.

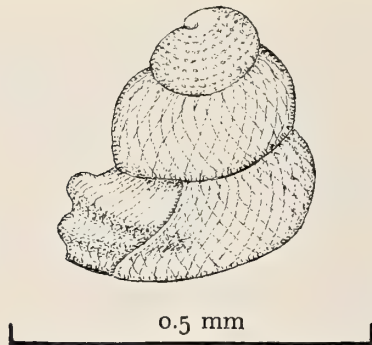


Figure 6

Protoconch of *Daphnella levicallis* Poorman, spec. nov. $\times 90$.

Holotype: San Diego Natural History Museum, SDNHM 81611.

Dimensions of the holotype: Height 17.3 mm (apex eroded), maximum diameter 7.2 mm.

Paratypes: Nine paratypes are in the Forrest and Leroy Poorman Collection; two paratypes are in the Carl and Laura Shy Collection, Seal Beach, California; four paratypes are in the Paul and Carol Skoglund Collection, Phoenix, Arizona; one paratype will be placed at the Academy of Natural Sciences of Philadelphia.

One additional specimen was dredged by Paul and Carol Skoglund in 100 m off Isla Danzante, Gulf of California.

The specific name is a Latin noun, masculine gender, and refers to the subsutural trace of the anal sulcus as a "smooth mountain path" much like the path up the Tower of Babel.

Discussion: All of the recognized west American *Daphnella* and the new species described here are very similar, differing only in size and details of ornamentation. The mechanism for developing the trace of the anal sulcus is observable on all. This subsutural band is also observable on the teleoconchs but is obscured except on *Daphnella retusa* McLean & Poorman, 1971, and the new species. Thickening of the outer lip occurs both internally and externally on the adults of all the species.

Both *Daphnella retusa* and *Daphnella levicallis*, spec. nov., occur in significant numbers off Estero San Carlos but differ in their bathymetric ranges and habitats. *Daphnella retusa* is found in 30 m on gravel bottoms; whereas *D. levicallis* is found in 100 m on shell and silt bottoms. *Daphnella levicallis* is larger, heavier, and of a darker color; the axial ribs are not obsolete on the body whorl, as they are on *D. retusa*, but extend nearly to the anterior canal. The ribs are crossed by strong spiral cords in prominent nodes not occurring on *D. retusa*. The trace of the anal sulcus is broader and flatter on the new species, with



Figure 7

Protoconch of *Anachis (Parvanachis) mullineri* Poorman, spec. nov. $\times 30$.

the axial ribs projecting slightly at their terminations to give a beaded effect to the shoulder.

Anachis (Parvanachis) Radwin, 1968

Type species: *Buccinum obesum* C. B. Adams, 1845.

The shell is small and obese, with a moderately high spire and flat-sided whorls with incised sutures. Body whorl and spire are of equal length. The apertural lip is thickened and denticulated. Sculpture is of prominent axial ribs crossed by spiral cords.

Anachis (Parvanachis) mullineri Poorman, spec. nov.

(Figures 4, 7)

Description: The shell is small and stout, consisting of a turritate protoconch of four smooth turns and a teleoconch of three and one-fourth whorls, terminating in a large, rounded, lip varix that decreases in size anteriorly. Transition from protoconch to teleoconch begins with weak, slanted ribs advancing anteriorly. The transition takes about one-half whorl when the ribs become longitudinal, rounded, and with equal interspaces. There are about 20 ribs on each whorl. The ribs are abruptly constricted just above the indented suture to leave widened areas in the interspaces. The ribs are rounded, protrude slightly above the shoulder, and are obsolete on the base. A spiral groove just below the indented suture cuts the ribs to produce a row of squarish beads. Below this is a region with no spiral sculpture. The middle half of the body whorl shows nine strong spiral grooves in the interspaces of the ribs. On the base, the spiral grooves override the diminishing ribs producing strong, flat-topped spiral cords. The entire surface of the teleoconch is covered with minute, spiral striae. The narrow aperture is somewhat trapezoidal. The outer lip is sharp, erect, and slightly crenulated by the spiral cords overriding the lip varix. Within the outer lip are six denticles. Columellar callus

is produced into a lamella with a chink behind, both of which extend to the end of the canal (chipped on the holotype). Within the aperture, along the pillar, is a longitudinal ridge of callus with six denticles. The anal sulcus is semicircular in cross section and slightly constricted by parietal callus. The sulcus penetrates the outer lip and varix at an angle of 60° with the axis and curves to terminate at an angle of 90°. The short, anterior canal is at an angle of 30° left of the shell axis, scarcely differentiated from the aperture, and broadly open to the right. The shell is light horn color with a band of darker brown above the periphery and a second indefinite band on the base.

Type locality: Bahía de Santiago, Colima, Mexico; 19°02'N Latitude, 104°28'W Longitude; five specimens dredged in 20 m on sand and gravel bottom.

Holotype: San Diego Natural History Museum, SDNHM 81612.

Dimensions of the holotype: Height 5.0 mm, maximum diameter 2.8 mm.

Paratypes: Four paratypes are in the Forrest and Leroy Poorman Collection.

Additional specimens in the Paul and Carol Skoglund Collection, Phoenix, Arizona, are from: Cuastecomate, Jalisco, dredged in 25–33 m; La Cruz de Juanacastle, Bahía de las Banderas, Nayarit, dredged in 20 m; Playa Novellero, Nayarit, diving in 8–12 m.

The specific name is chosen in recognition of David K. Mulliner, San Diego, California, a good friend known to all for his generous contributions of time and talent to the field of malacology.

Discussion: The massive lip varix and the unusual anal sulcus curving across it, together with the erect lamella along the pillar, are distinctive and make further comparison with other existing taxa unnecessary.

ACKNOWLEDGMENTS

I wish to recognize with thanks the contributions of Anthony D'Attilio, San Diego Natural History Museum, who made the protoconch drawings, and David Mulliner for technical assistance in preparing the illustrations.

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The Biology of the Northeastern Pacific Turridae.

III. The Habitat and Diet of *Kurtziella plumbea* (Hinds, 1843)

by

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Abstract. The habitat, diet, and some reproductive and mortality factors were determined for *Kurtziella plumbea*, a shallow-water turrid gastropod from the Puget Sound region. In a shallow subtidal area with four depth-related habitats, it was found more often in upper habitats, although all of the habitats available were sandy and had similar sedimentary characteristics. In a deeper area, it was found primarily in areas of silty mud. *Kurtziella plumbea* is a predator of polychaetes. At the shallow site, it specialized on the oweniid *Owenia fusiformis* and spionids. In the deeper area, it was more generalized, but the cirratulid *Tharyx multifilis* was the most abundant prey item.

Egg capsule deposition occurred in the spring. There were no nurse eggs, and the time until veligers left the capsule was about 18–20 days. Settlement and metamorphosis were not observed. Growth rates of 1 to 2 mm/yr for median-sized individuals, and 3 to 4 mm/yr for small individuals were indicated.

Potential predators may include crabs and fish, but mortality factors were not conclusively determined.

INTRODUCTION

THE MOST WIDELY distributed turrid gastropod in the shallow northeastern Pacific is *Kurtziella plumbea* (Figure 1), which is found from Mazatlán (McLEAN in KEEN, 1971) to southcentral Alaska (Shimek, unpublished data). I examined two populations of *Kurtziella plumbea* (hereafter as *Kurtziella*) to determine habitat, dietary requirements, and aspects of predatory and reproductive behavior. I attempted to determine some of the reasons why this particular snail is so widespread. Two mutually contradictory statements about this species were examined. (1) The species is generalized in both its use of habitats and prey, and thus it can be found in many habitats. In effect, it would be a successful "Jack-of-all-trades." (2) The species is specialized in habitat and/or diet, but the array of suitable habitats is widespread, thus permitting the snail to be widespread. Several major questions were addressed. (1) What is the relationship of diet to the potential dietary resources present? (2) Are these animals dietary or habitat

specialists or generalists? (3) What is the effect of these predators upon their prey populations? (4) Are there any particular traits that limit their choices of habitats or prey?

MATERIALS AND METHODS

Study Sites

All sites were subtidal, since *Kurtziella* is rarely intertidal in this region. Two major study sites were chosen: Windy Point in Dyes Inlet in lower Puget Sound and off the University of Washington Friday Harbor Laboratories dock on San Juan Island (Figure 2). Additional specimens were collected from many other localities, particularly in the San Juan Islands (SHIMEK, 1977); however, at these latter sites I collected only distributional data; quantitative data were seldom obtainable. Distributional information was gathered by dredge or bottom tow. All quantitative field work was done using SCUBA.

The Windy Point area, WP (47°37'25"N, 122°40'30"W), ranges from -1.5 m to -9.0 m below MLLW. It is a topographically homogeneous, sandy subtidal region unbounded laterally and divisible into four visually distinctive habitats: upper bench, upper slope, lower slope,

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Figure 1

A. *Kurtziella plumbea* (Hinds, 1843). Scale in millimeters. B. Radular teeth of *Kurtziella plumbea*. Scale bar = 10 μm . These are stabbing toxoglossan teeth used individually to pierce the prey and to introduce venom.

and lower bench, based upon the degree of slope, depth, and algal cover (SHIMEK, 1982). *Kurtziella* is found there with two other turrids, *Ophiidermella inermis* (Hinds, 1843) and *Oenopota levidensis* (Carpenter, 1864).

The Friday Harbor Laboratories site, FHL (48° 32'38"N, 123°00'50"W), is topographically diverse, containing five visually distinctive habitats: wood chips, rock, shell fragments, and shallow and deep areas of silty mud.

The site is located from -10 m to -25 m below MLLW. No discontinuities limit the site except at the upper edge where the boundary is established by the lower edge of an eelgrass, *Zostera marina* L., 1753, bed. No turrids were found in either the eelgrass or wood-chip areas in preliminary observations, consequently no quantitative sampling was done in either habitat. The remaining habitats were sampled quantitatively.

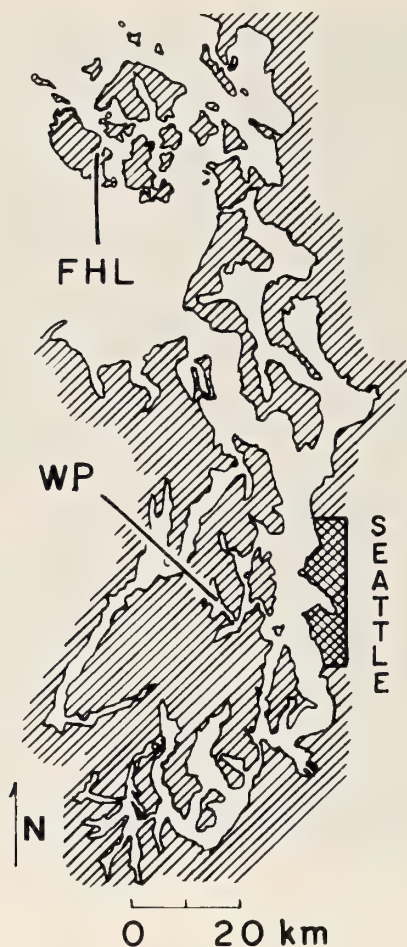


Figure 2

The Puget Sound region of Washington state showing the study sites.

Habitat Analyses

At the major sites, the physical and biological properties of the habitats were examined in detail. Sediment particle-size distributions were quantitatively determined and the remainder of the sample was washed through a 0.5-mm sieve. The animals were removed and sorted by taxon. Gastropods and polychaetes were identified to species whenever possible. Other taxa were identified to class and counted, but not detailed further (see SHIMEK, 1982, for a more complete description of sampling methods).

Sediment parameters were tabulated and statistically compared between and within the areas. Seasonal variability of the sediment particle distributions was insignificant, thus no seasonal comparisons were made (SHIMEK, 1982).

Polychaete assemblage abundances for each habitat were determined by the quantitative, infaunal sampling, and

statistical comparisons were made between and within habitats on a seasonal basis (SHIMEK, 1982).

Turrid Distribution, Collection, and Processing

Periodic transect studies from November, 1973, until December, 1975, were used to determine turrid distribution, seasonal or other distributional changes, and to provide a reference for the quantitative infaunal samples. The significance of *Kurtziella* distributions compared to random habitat utilizations were calculated using log-likelihood ratios (G-tests) (SOKAL & ROHLF, 1969).

A hand-held, semiquantitative dredge was used at FHL to determine the relative fraction of the turrid populations buried in the sediment. Simultaneous, parallel, surface-transect surveys were conducted to compare the number of snails buried and on the surface.

Kurtziella collected from FHL and WP were individually washed in sea water, isolated for up to a week, and feces were collected. The snail was then measured to the nearest 0.1 mm, and marked (SHIMEK, 1982). After marking, the animal was returned to fresh sea water at ambient sea-water temperature and observed to assure no noticeable effects of measuring and marking. The animal was then transferred to a "holding" aquarium and maintained in an artificial habitat similar to the normal one. All apparently healthy animals were returned to their habitat, albeit seldom to the point of capture, within two weeks. Measuring and marking mortality was about five percent.

Following marking and measuring, any particulate material remaining in the collecting jar was placed on a slide, dried, mounted in polyvinyl lactophenol (A. Kohn, personal communication), and examined microscopically. Identification of all fecal material was attempted. Feces consisted of mucus, radular teeth of the same animal, diatom frustules, and polychaete remains. Preliminary gut analysis by dissection indicated polychaetes swallowed whole to be the only prey. Thus only polychaete remains consisting of setae, jaws, and occasional cuticular strips were accepted as indicators of feeding. These remains were identified by comparison with descriptions, drawings, and setal preparations of known animals, identified with standard references (SHIMEK, 1982). Dietary heterogeneity was measured using H' (KOHN & NYBAKKEN, 1975). Turrids collected from other localities were preserved and their habitats noted, if the collecting was done with SCUBA, but no dietary analysis was attempted.

Size-frequency histograms were constructed for both populations. These were normalized to percent collected to facilitate comparison between populations because of varying sample sizes. For the purpose of determining growth rate, collections were considered quarterly: November through January as Winter; February through April as Spring; May through July as Summer; and August through October as Autumn. Generally these samples were too small and/or variable for quantitative determinations of recruitment cohorts (BLISS, 1967); however, I

attempted to use seasonal shifts in histogram peaks to estimate growth rates.

Laboratory Experiments

A substrate-choice chamber was constructed, and filled to a depth of 2 cm with sediments (SHIMEK, 1982). The choices were sediments with a particle-size distribution from 0.250 to 0.500 mm, and a distribution in excess of 2.00 mm. Both sides had all detectable biota removed. Animals were placed in the chamber and one week later they were collected and their positions noted. These data were analyzed using cumulative binomial probabilities.

Egg capsules were collected from the jars in which the turrids were stored. Capsular dimensions were measured, the number of eggs per capsule was counted, and the egg diameters were measured (SHIMEK, 1982). The capsules were examined periodically. After hatching, the veligers were fed a mixture of *Isochrysis* sp. and *Dunaliella* sp.

RESULTS

Habitat Descriptions

Windy Point: The four Windy Point habitats have been described in detail elsewhere (SHIMEK, 1982). Briefly, these habitats were sandy, with moderately well-sorted, unconsolidated sediments. They were similar to each other and to the nearby sandy low intertidal areas. Algal cover in the shallower (depth < -5 m) areas varied seasonally, being very abundant in the late summer, and was mostly ulvoid algae. In the deeper areas the algal cover consisted of various red and brown algae and was less variable or dense.

Friday Harbor Laboratories: The FHL habitats are also described in SHIMEK (1982). Of the four major turrid habitats, only the rock areas could not be sampled quantitatively for infauna and sediment. Of the three unconsolidated-sediment areas, only the lower mud was physically different, having a distinctly smaller median-sediment-particle size.

Biology of *Kurtziella* at Windy Point

Kurtziella was associated with the turrids *Ophiidermella inermis* and *Oenopota levidensis* at WP. All three were distributed in patches, and because of this, the mobility of these animals, and the lack of physical boundaries to the study area, no adequate estimates of population sizes could be made. Capture and transect observational frequencies did, however, give an estimate of relative population sizes. I collected or observed 254 *Ophiidermella inermis*, 134 *Kurtziella*, and 108 *Oenopota levidensis*. *Kurtziella* and *Oenopota levidensis* appeared to have roughly equivalent populations. During quantitative surveys, the density of *Kurtziella*, when found, varied from 0.01/m² to 0.16/m². No seasonal trends in abundances or habitats utilized were seen, but *Kurtziella* was found more often in the shallower

Table 1

Windy Point *Kurtziella plumbea* habitat utilization.

Habitat	Proportion of total area	Proportion of turrids per area	Proportion of turrids observed - proportion expected
Upper bench	0.25	0.34	+0.09
Upper slope	0.25	0.26	+0.01
Lower slope	0.25	0.17	-0.08
Lower bench	0.25	0.24	-0.01
Number observed			134
Significance (G-test)	G = 9.40	P < 0.05	

areas at WP (Table 1). The sediment-particle distributions were not significantly different among most of these areas (SHIMEK, 1982). Depth was probably not a factor as *Kurtziella* was found in the deeper areas at FHL (Table 2).

There was a patchy distribution of the polychaete fauna at WP, particularly regarding the turrid prey species *Owenia fusiformis* delle Chiaje, 1844, which was dense only in the upper bench areas, and *Polydora socialis* (Schmarda, 1861), which was more widely distributed than *O. fusiformis* (Table 3). There was no seasonal pattern of predation at either site, consequently the prey-polychaete-abundance data were pooled. The high sample variability reflected seasonal abundance patterns for the worms; see

Table 2

Friday Harbor Laboratories *Kurtziella plumbea* habitat utilization.

Habitat	Proportion of total area	Proportion of turrids per area	Proportion of turrids observed - proportion expected
A. All habitats			
Upper mud	0.25	0.06	-0.18
Shell fragments	0.34	0.35	+0.01
Rock	0.05	0.06	+0.01
Lower mud	0.36	0.52	+0.16
Total number observed			48
Significance (G-test)			P < 0.01
B. Lower habitats only			
Shell fragments	0.45	0.38	-0.07
Rock	0.07	0.07	0.00
Lower mud	0.48	0.56	+0.08
Number observed			45
Significance (G-test)			n.s.

Table 3
Density of prey species (mean number/m² ± 1 SD).

A. Area: Windy Point				
Habitats:	Upper bench	Upper slope	Lower slope	Lower bench
Prey species				
<i>Owenia fusiformis</i>	713 ± 413	197 ± 375	9 ± 22	0
<i>Polydora socialis</i>	843 ± 907	661 ± 591	468 ± 440	268 ± 440
<i>Spiophanes berkeleyorum</i>	0	0	5 ± 16	0
B. Area: Friday Harbor Laboratories				
Habitats:	Upper mud	Shell fragments	Lower mud	
Prey species				
<i>Myriochele oculata</i>	6 ± 19	0		0
<i>Cirratulus cirratus</i>	31 ± 56	23 ± 37		20 ± 37
<i>Tharyx multifilis</i>	136 ± 125	79 ± 77		157 ± 85
<i>Spiophanes bombyx</i>		not sampled		

SHIMEK (1977, 1982) for more complete listings of the polychaetes.

Kurtziella was found to be widely, but unevenly, distributed in the Puget Sound region. I dredged and/or surveyed by SCUBA 40 different sites and *Kurtziella* was found in only six of them (SHIMEK, 1977). All six were characterized as sandy or sandy-mud habitats.

Dietary Analysis

Dietary information obtained by fecal examination is summarized in Table 4. *Kurtziella* at WP ate three species of identified polychaetes. Densities of the most common prey, *Owenia fusiformis*, fluctuated dramatically in all but the upper-bench area, and this worm was absent from the lower-bench area completely (Table 3).

Predation on *Kurtziella* at WP

In the WP-slope habitats predation by crabs upon the snails may have been an important factor. Two predatory

crabs were present, *Cancer gracilis* Dana, 1852, and *C. productus* Randall, 1839, although specimens of the latter were uncommon, probably because of too few suitable refuges (SHIMEK, 1982). During the summer when the crabs were common, *Kurtziella* became rare (Figure 3). Consequently, no laboratory verification of the attractiveness of *Kurtziella* as a prey item was attempted. *Cancer productus* will eat both *Oenopota levidensis* and the larger *Ophiidermella inermis* in the same area, and *Cancer gracilis* may eat small snails of all types. As *Kurtziella* was smaller than the other turrids at WP, it was a likely prey item for both crabs.

Biology of *Kurtziella* at Friday Harbor Laboratories

The turrid assemblage at FHL is diverse, in addition to *Kurtziella*, nine other turrids in three other genera are found there (SHIMEK, 1982, 1983). Habitat utilizations were determined from transect surveys. As with the other turrids at FHL, *Kurtziella* was less common in the upper-mud area than would be expected if it was randomly distributed (SHIMEK, 1982, 1983). If the upper-mud area is considered to be a boundary area that is incompletely utilized, and the data from this habitat are excluded, *Kurtziella* was collected most frequently in the lower-mud habitat (Table 2). When found, *Kurtziella* had measured abundances from 0.01/m² to 0.05/m².

The polychaete fauna at FHL was diverse and sparse. The most abundant turrid prey, *Tharyx multifilis* (Moore, 1909), were present in most of the samples and habitats (Table 3). The infaunal assemblages from all of these habitats were similar in the summer, but in the winter the upper- and lower-mud areas had many differences (SHIMEK, 1982).

The substrate-preference experiments gave conclusive results, even with the small number of individuals available at any one time for each test. Of the animals tested,

Table 4

Results of fecal sample analysis of *Kurtziella plumbea*.

Area:	WP	FHL	Total
Prey species			
<i>Myriochele oculata</i>		1	1
<i>Owenia fusiformis</i>	13		13
<i>Polydora socialis</i>	1		1
<i>Spiophanes berkeleyorum</i>	2		2
<i>S. bombyx</i>		1	1
<i>Cirratulus cirratus</i>		1	1
<i>Tharyx multifilis</i>		3	3
Unidentified polychaetes	1	4	5
Number of snails examined	139	110	249
Percent feeding	12.2	9.1	10.8
H' (identified prey only)	0.60	1.24	1.36

17 animals made choices; 13 chose the sediment with smaller particle-size distribution (0.250 mm–0.500 mm), whereas only 4 chose the sediment with particles larger than 2.00 mm. The two-tailed binomial probability of a deviation this large or larger, given an equal probability of choice, is 0.049.

The hand-held, semiquantitative dredge was used infrequently as it resulted in substantial habitat damage. Data from these dredge samples indicated equivalent numbers of *Kurtziella* buried and on the surface at the times of the surveys. During the surface surveys, five *Kurtziella* were found in 583 m². Simultaneous dredging parallel to, but 2 m lateral to the surface-survey-transect lines collected one *Kurtziella* in 116.6 m² dredged to a depth of 0.10 m.

Dietary Analysis

Relatively few animals were found eating (Table 4), and no seasonal dietary trends were evident. At WP, *Kurtziella* was most often feeding on *Owenia fusiformis*, although spionids were also found in the diet. At FHL, no such clear-cut pattern of specialization was evident, and the snails had a more catholic diet consisting of cirratulids, spionids and oweniids. In contrast to the prey distribution at WP, the major prey taxon at FHL, the Cirratulidae, was common in all habitats (Table 3).

Kurtziella Reproduction

Collection and confinement for fecal-sample examination acted as stimuli for egg-capsule deposition in some turrids (SHIMEK, 1982, 1983). Eight individuals of *Kurtziella* deposited egg capsules in captivity in March, April, and May, 1975 (Table 5). Single females deposited from one to three capsules. Capsules were smaller than the egg capsules of either *Oenopota* or *Ophiodermella*, and contained fewer, smaller eggs (SHIMEK, 1982, 1983). The egg capsules were deposited on the inside of the collection jar at the junction of the lateral and bottom surfaces. The eggs in 10 capsules hatched after about 18–20 days. As with *Oenopota* and *Ophiodermella*, there were no nurse eggs, and the number of veligers leaving the capsules was the same as the original number of eggs deposited. Four capsules contained eggs that did not develop at all. Presumably the stimulus for oviposition was so strong that unfertilized eggs were deposited in the capsules. These capsules appeared normal in all other respects. No egg capsules of *Kurtziella* were seen in the field.

Life Histories

Seasonal size-frequency distributions can be examined for indications of growth rate, recruitment, and sizes of individuals in the population. A comparison of the FHL and WP populations yields some interesting observations. The WP population was composed of distinctly smaller individuals with virtually no animals exceeding 12 mm

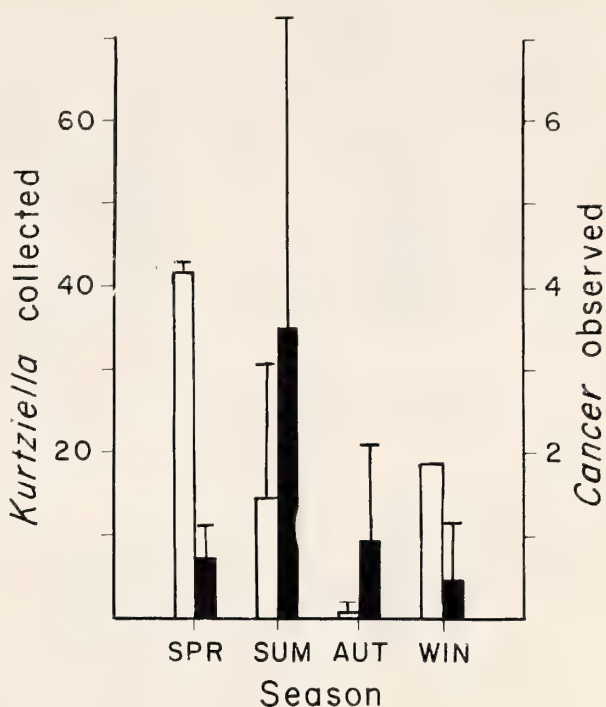


Figure 3

Mean (± 1 SD) number of *Kurtziella plumbea* (open bars) collected and mean number of *Cancer gracilis* (black bars) observed (per 25 m²) by season. All habitats and seasons were pooled. Data are for Spring, 1974, through Autumn, 1975; therefore, *Kurtziella* was collected in only one winter.

total length (Figure 4). On the other hand, the FHL population was composed of larger animals, with almost no animals below 10 mm total length (Figure 5). Neither population showed appreciable seasonal shifts in the size-frequency histograms, although in both populations the mean individual length increased from spring to winter, and dropped again the following spring. The pattern of changes in the mean sizes in both distributions was virtually identical although consistently displaced by the amount the two populations differed in mean length. Examination of the seasonal shifts for both populations in-

Table 5

Kurtziella plumbea reproductive information.

	Mean capsule dimensions (μ m)		Mean egg	
	Length	Width	Number/capsule	Diameter (μ m)
	230 \pm 34	186 \pm 22	180 \pm 43	137 \pm 8
Number examined	13		6	9
Number of capsules hatching:	10			
Mean number of days in the capsule:	19.3 \pm 1.16 days			
Maximum length of survival post hatching:	27 days			

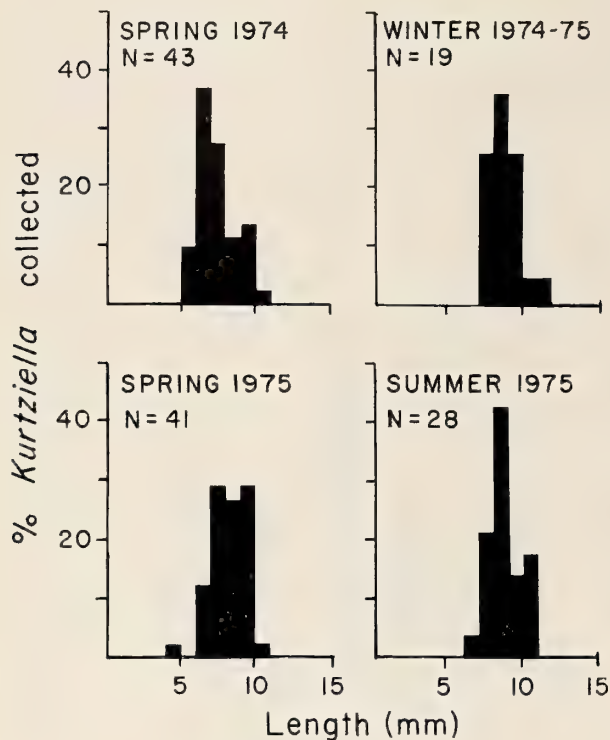


Figure 4

Windy Point seasonal size-frequency distributions. In seasons not shown (Summer, Autumn, 1974) too few snails were observed to make the data meaningful.

dedicated a growth rate, for a 7–8 mm-long individual, of about 1.5 mm/yr. No marked animals were recaptured from the WP population. Five previously marked individuals were recaptured from the FHL population. Three decreased in total length, and two increased. One of those two had grown 0.5 mm in 287 days, indicating a growth rate of less than 1 mm/yr. This individual was 11.9 mm long when initially captured, however; and the larger individuals may grow more slowly than smaller ones, which was a pattern seen in the other turrids examined from these areas (SHIMEK, 1982, 1983).

In both populations, distinctly smaller animals were recovered only in the spring. If this species has a faster growth rate in the smaller size classes, the 4–6 mm-long individuals recovered in the spring of one year may represent larvae settling the previous summer. Growth rate determinations were difficult for these animals due to their small size, the wide variation in lengths, and the lack of more than one clearly defined peak in the size-frequency histograms.

DISCUSSION

As with sympatric turrids in the genera *Oenopota* and *Ophioderrella*, *Kurtziella* eats tube-dwelling polychaetes;

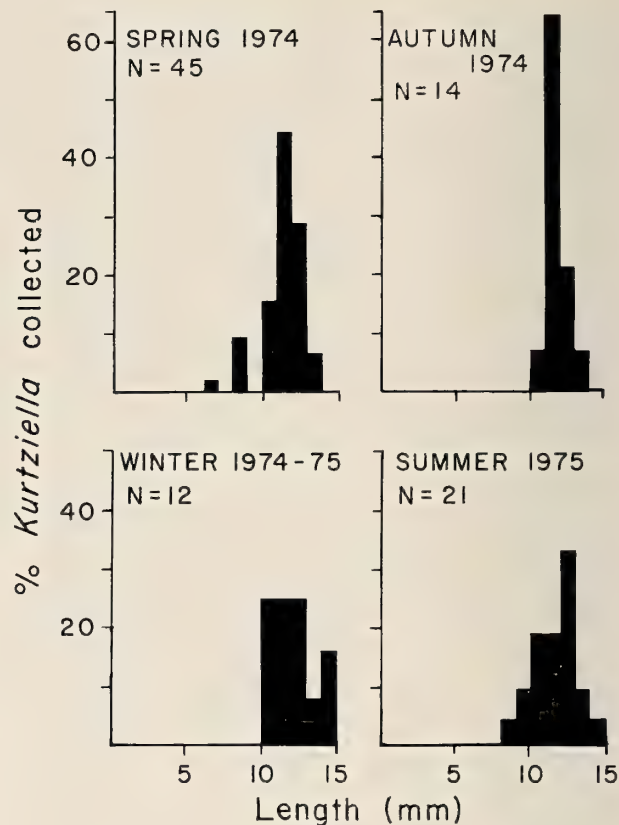


Figure 5

Friday Harbor Laboratories seasonal size-frequency distributions. In seasons not shown (Summer, 1974; Spring, 1975) too few snails were observed to make the data meaningful.

but the range of prey taken is quite broad, from oweniids to cirratulids, although at WP, *Owenia* predominates. The diversity of acceptable prey may be less at WP, possibly limiting animals in this population to fewer potential prey species. This might also explain the tendency of the *Kurtziella* to be found in areas where *Owenia* was common. Because manipulative experiments were not attempted, the turrid's effect on its prey is uncertain, but predation by *Kurtziella* alone probably did not have any substantial impact on the populations of its prey. The species appeared to have ample food sources; indeed, *Tharyx multifilis*, its major food, was one of the most abundant polychaetes in the FHL areas, and *Owenia fusiformis* was very abundant in some habitats at WP.

Kurtziella appears to be restricted to sandy or sandy-mud habitats and is rarely found on nearby rocky or shell-fragment habitats. Additionally, it seems to have substantial latitude in potential prey, although more data are needed to confirm this. The skewed distribution of *Kurtziella* at WP may indicate tracking of its most common prey species, *Owenia fusiformis*. *Owenia* was rarely found

below the upper-slope areas, and *Kurtziella* is more common in these upper areas than in the lower ones.

Predatory effects on this species are difficult to determine. The major predators in the WP area are inferred to be the crabs, *Cancer gracilis* and *C. productus*. Both crabs were common and have been shown to eat other, larger, turrid gastropods in the same area (SHIMEK, 1982, 1983). Nonetheless, no direct evidence of this predation was encountered. *Kurtziella* is a small snail with a relatively fragile shell, and attacks by these large crabs probably result in the complete destruction of the shell. Unlike *Ophiodermella* and *Oenopota* species, *Kurtziella* does not show any significant tendency to bury; this may result in substantial mortality when the predatory crabs are common. The relative rarity of the species at WP during and after the summer population peak of the crabs is likely the result of predation. The smaller mean length of individuals in the WP population, compared to the FHL population may result from some size-selective predation by the crabs on larger snails. Immigration from deeper habitats where the crabs are less common is probably responsible for the recovery of the population.

Mortality effects at FHL are unknown. During the course of study, over 100 turrid shells were recovered with hermit crabs in them. These shells proved useful in determining some of the causes of mortality of some of the other turrids in the region (SHIMEK, 1982, 1983), but no *Kurtziella* shells were recovered. This may be indirect evidence of predation by crushing predators like crabs, which can sometimes be found in the FHL habitat. Some fishes may also eat the snails. Except for *Luidia foliolata* Grube, 1866, predatory asteroids are uncommon in the area.

In both populations, the snails appear to have a defined maximum size of about 15 mm. Growth may cease or slow as the animals approach this size, thus making measurement of growth rates difficult. There is no indication of semelparity in this species. After spawning, the females appear healthy, and all were marked and returned to their habitat.

In conclusion, *Kurtziella* requires sandy or sandy-mud habitats, and overall is a dietary generalist, although it may specialize in some populations. Thus, the hypothesis that *Kurtziella plumbea* is a "Jack-of-all-trades" for both diet and habitat is rejected. It is likely that suitable sandy or sandy-mud habitats are widespread on the Pacific coast of North America; this turrid should be expected in many of them. That this species will be rarely found in rocky or shell-fragment areas is also predicted.

ACKNOWLEDGMENTS

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Editor's note: After the issue had gone to press, we were informed that the paper referred to as "Shimek, 1982" throughout the present article was published in 1983.

Flow Through and Around the Abalone

Haliotis kamtschatkana

by

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Abstract. Fluorescein dye streams released along the shell and at the shell openings of living and dead abalones revealed the lines of water flow around and through the shell. Regardless of ambient flow speed, water entered the shell of live abalones at a region to the left of the left cephalic tentacle and also through the one or two most anterior shell openings and exited through the two or three most posterior openings. An identical flow pattern occurred through the shell of dead, intact animals when placed in an ambient flow of 6 cm/s, regardless of whether the anterior end faced upstream or downstream. Since the exhalent openings occur at the site of the shell at which the ambient streamlines are maximally compressed, they experience a reduction in pressure relative to the anterior, inhalent ones. Thus, the design of its shell may enable the abalone to take advantage of an induced flow to move water more efficiently through its mantle cavity.

INTRODUCTION

Haliotis kamtschatkana Jonas, 1845, the pinto abalone, must deal with changes in environmental flow while maintaining respiratory currents through its mantle cavity. These animals have a row of four to six openings through the dorsal shell surface that, according to earlier workers (GARSTANG, 1928; CROFTS, 1929; YONGE, 1947) evolved to prevent wastes released in the mantle cavity from moving forward over the gills and head. In addition to creating a flow through its shell by beating the cilia of its gills, *Haliotis* could use environmental currents to help drive water through its mantle cavity. Such an induced flow requires that the inhalent openings encounter fluid at a pressure higher than that of the exhalent openings (VOGEL, 1981). MURDOCK & VOGEL (1978) found that the keyhole limpet, *Diodora aspera*, experiences such an externally driven flow and may use this flow to move water more efficiently through its mantle cavity. *Haliotis kamtschatkana* lives in areas of surge and strong currents (Richard Emlet, personal communication), where it seems possible that its series of shell openings could be exposed to pressure differences sufficient for induced flow to occur. To visualize the paths that lines of water flow follow around and through abalones I combined information from dissections, dye streams, and flow velocity measurements taken in and around living and dead individuals.

MATERIALS AND METHODS

Five adult individuals of *Haliotis kamtschatkana* ranging in maximum aperture diameter from about 9–12 cm and collected from various sites in the Friday Harbor region of San Juan Island, Washington were used. The flow these animals normally encounter may range from 0–150 cm/s or more (Kenneth Collier, personal communication).

To relate the external flow information to the anatomy of the animal, I dissected both fresh and narcotized animals. To narcotize, I added increasing volumes of a 7% $\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$ solution to animals in cooled (8°C) sea water until the epipodial and cephalic tentacles no longer retracted when touched.

To visualize the flow of water qualitatively through and around *Haliotis kamtschatkana*, I used a stream of fluorescein dye controlled by a micro dye injector (an adjustable syringe fitted with a drawn plastic tip and moved by a micromanipulator). Pencil marks at 1-cm intervals along the edge of the shell served as reference points for following dye paths, technically referred to as streaklines. Dye was released at each of these points along both sides of the animals as well as at various sites near the anterior and dorsal surfaces of the shells. Studies of animals in flowing and in still water took place in a 15-cm flow tank designed by VOGEL & LABARBERA (1978).

Observations of induced flow were made on animals

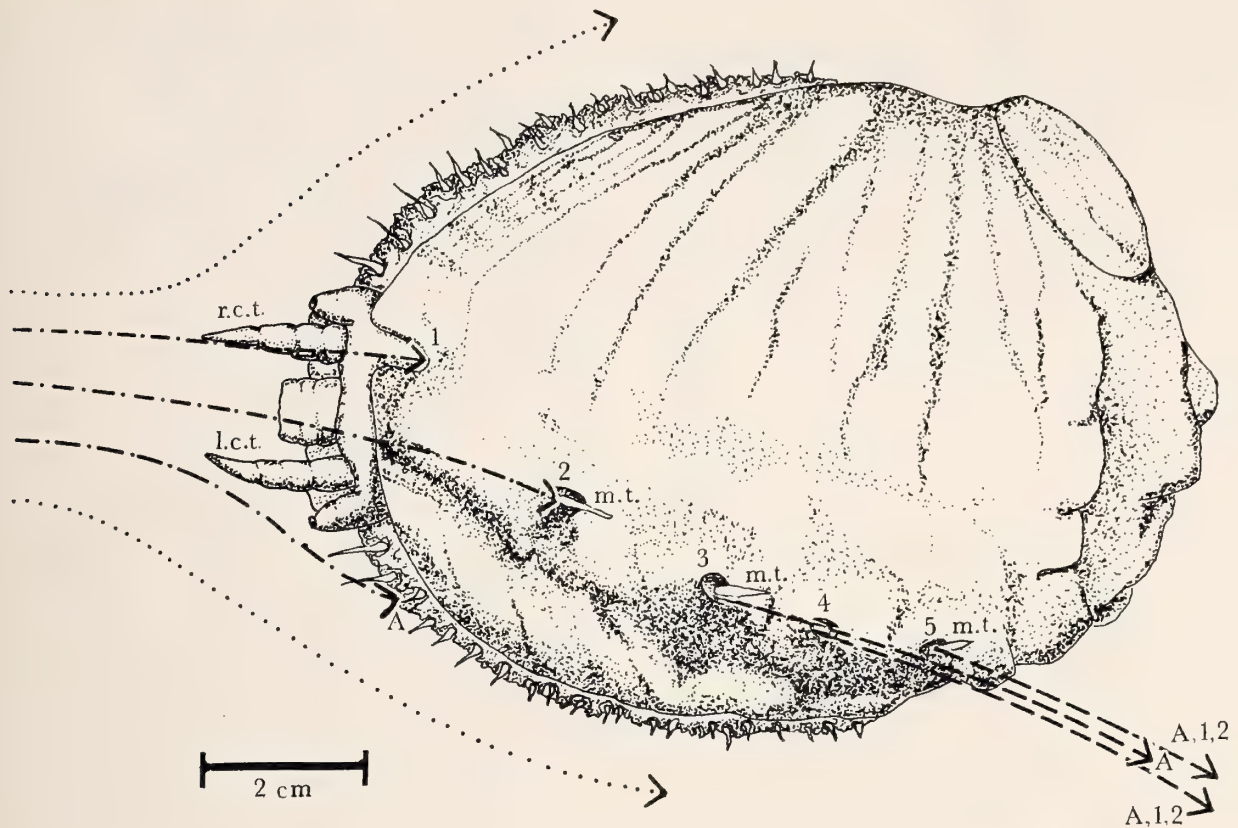


Figure 1

Diagram of flow through and around an abalone facing upstream in an ambient flow of about 6 cm/s. l.c.t.: left cephalic tentacle; r.c.t.: right cephalic tentacle; m.t.: mantle tentacle; A: site at left side of shell where water enters mantle cavity; 1, 2: anterior, inhalent shell openings; 3, 4, 5: posterior, exhalent shell openings; dot-dash lines (---): inhalent streaklines; dashed lines (---): exhalent streaklines; dotted lines (····): flow along anterior end and side of shell. Letters and numbers at ends of exhalent streaklines correspond to the points at which streaklines may have entered the mantle cavity.

that were first relaxed in MgCl_2 as above and then quickly frozen to -20°C by placing them in the bottom of a cryostat. The animals were returned to ambient sea water temperature before any data were taken.

RESULTS

Dye released at specific points around an animal facing upstream in an ambient flow of about 6 cm/s formed a repeatable set of streaklines (Figure 1). Water approaching the anterior edge of the shell was either deflected upward (perpendicular to the general direction of flow), straight upstream (180° to the general flow), or was passed in a series of vortices along either side of the shell. Flow contacting the shell at either side continued downstream close along the shell and then became caught in the turbulent backwash behind the animal. In ambient flows ranging from approximately 2–15 cm/s the streaklines

did not appear to be velocity-sensitive, although there was more turbulence at higher speeds.

Abalones accepted incoming water only at specific sites along the shell (Figure 1: A, 1, 2). At the lower edge of the shell, water entered in a region 1–3 cm to the left of the left cephalic tentacle. It appeared that the animals could control the entrance at this region by waving the left cephalic tentacle. Dye released in the region between the two cephalic tentacles sometimes traveled along the edge of the shell, over the left tentacle and eye, and into the mantle cavity. At other times under the same flow conditions it was deflected by the tentacles and passed downstream alongside the shell.

The two most anterior openings of the shell also served as sites of water intake. Depending upon the position of the mantle tentacles, dye released upstream, above, or beside these openings entered the mantle cavity. If the anterior opening was incomplete, resembling a fold at the

edge of the shell, dye released just below its dorsal edge proceeded into the mantle cavity, while dye released at other points within the same region traveled up and out away from the shell, as mentioned above.

Only the two or three most posterior openings on the top of the shell served as the animals' exhalent passages from the mantle cavity. In all cases the penultimate opening (4 in Figure 1), which ordinarily has no mantle tentacle, was the chief channel for wastes and exhalent water flow. The most posterior opening was often partially sealed and always had a tentacle, both of which reduced its output volume and rate. The center-most opening, which usually had a mantle tentacle, tended to be weakly inhalent, although at times dye streams also exited from it. Dye streams usually exited from the posterior or from the right side of the exhalent openings and were laminar.

Except at regions of exhalent and inhalent currents, dye released at the sides of animals standing in still water did not move. The inhalent and exhalent regions were at the same locations in animals in still water as they were in moving water.

Dye released at the inhalent openings of dead, intact abalones facing upstream in a flow of about 10 cm/s entered the mantle cavity at the site of release and exited through one of the exhalent openings. Shells of the same animals oriented downstream had similar patterns of flow through them, although the rate of the induced flow was not as high. In either orientation, dye released near exhalent openings did not enter the shell, but continued downstream.

DISCUSSION

Although earlier reports indicated that water enters the abalone mantle cavity only under the margin of the shell and mantle flap on either side of the head (STEPHENSON, 1924; CROFTS, 1929; YONGE, 1947), it is well known now that in at least some species the first hole serves for water intake as well (*e.g.*, ABBOTT & HADERLIE, 1980, p. 233). In *Haliotis kamtschatkana* the streaklines show that flow enters the mantle cavity in a restricted region to the left of the head and through the first, and sometimes second, shell opening. Only the posterior openings are exhalent, and they are the only channels by which water and excretory products may exit the mantle cavity.

The fact that the shell of a dead animal shows flow patterns through its openings similar to those of a live animal suggests that by its design, the animal may take advantage of an induced flow. Because of the shell shape, the exhalent openings lie in the region at which the streamlines over the shell are maximally compressed, leading to a reduction of pressure over the posterior openings relative to the anterior ones, which should cause the fluid to enter at the front and to exit at the rear (VOGEL, 1981). Location of openings relative to any wake formed and the geometry of the openings may also determine local pressure, but these aspects of flow were not investigated.

The orientation of the openings may further enhance the induced flow. As openings form at the anterior edge of the shell, they face the oncoming flow when the animal is facing upstream, and thus encounter dynamic pressure, or the pressure created due to stopping fluid (VOGEL, 1981). As the shell grows and new openings are added, older openings rotate relative to a horizontal surface, becoming more nearly parallel to flow, so that by the time they reach the central region of the shell and begin to function as exhalent openings they experience the reduced pressure described above. Thus as an animal grows, each opening performs first an inhalent and later an exhalent function. I noticed that on each animal there is one opening (or sometimes two) that may be both slightly inhalent near its anterior edge and exhalent near its posterior edge. Such transitional openings are located on the cusp of the shell and are oriented at an angle intermediate to openings that are strongly inhalent or exhalent. It may be that there is some angle at which an opening may no longer serve as an entrance to, and another at which it may begin to serve as an exit from, the mantle cavity. It is also possible that the cephalic and mantle tentacles may valve the openings and help control the direction and rate of flow.

Since induced flow may occur whether animals are facing upstream or downstream, they may need only be parallel to the general direction of surge to take advantage of it. This would make induced flow useful in regions of surge where flow reversal is common. It would be valuable to know if abalones orient to flow in their natural habitat and to what degree orientation is necessary for utilizing induced flow.

Traditionally, workers have believed that the openings in an abalone's shell evolved primarily as a way to avoid mixing fresh inhalent water with waste-laden exhalent water. I have shown that in addition to eliminating this problem, the shell determines the path by which water will enter, as well as exit, the mantle cavity. Whether or not this design increases the efficiency of moving water through the mantle cavity will require a study of the energetics of water movement.

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Shell Strength in *Corbicula* sp. (Bivalvia : Corbiculidae) from the Potomac River, Maryland

by

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Abstract. Forces required to crack intact shells of the freshwater Asiatic clam, *Corbicula* sp., were determined. They are higher than those which crack the wedge clam, *Rangia cuneata*, a globose, strong-shelled, oligohaline bivalve. Asiatic clam shell shape and strength may explain published data on crayfish predation on this animal in Oklahoma and Tennessee, in which predation was successful only on clams less than 6 mm in size or those with holes in the shell. Strong shells may also help prevent damage during periods of high river flow or strong water movement.

INTRODUCTION

CLAMS OF THE ASIATIC genus *Corbicula* were apparently introduced to western North America early in this century, becoming widespread in the ensuing years (BRITTON & MORTON, 1979; COUNTS, 1981). Recently, laboratory experiments by COVICH *et al.* (1981) revealed that two species of freshwater crayfish were able to feed only on specimens of *Corbicula* that were less than 6 mm in size or that had damaged (perforated) shells. The Asiatic clam is globose in shape and the shell is relatively thick, giving the impression of strength. MACKIE (1978) noted that the thickness of the shell of *Corbicula fluminea* was greater than the shells of 22 other species of sphaeriacean bivalves he investigated.

In an earlier study of crustacean predation on estuarine bivalves, we examined shell strength of eight species of clams (BLUNDON & KENNEDY, 1982). Here we present measurements of shell strength of the Asiatic clam, compare them with the strength of the estuarine bivalves, and relate the results to the findings of COVICH *et al.* (1981) concerning crayfish predation on *Corbicula*.

TAXONOMY OF EXPERIMENTAL ANIMALS

There has been much confusion associated with the taxonomy of *Corbicula* in North America, with BRITTON & MORTON (1979) having declared the species to be *Corbicula fluminea*. However, HILLIS & PATTON (1982) have presented evidence that two species of *Corbicula* (a "white form" and a "purple form") are present in the Brazos River, Texas. The specimens we tested in this report resembled the "white form" in color of nacre. Our specimens were collected from the Potomac River at Whites Ferry, Maryland (approximately 39°09'N; 77°31'W) in shallow water close to the river bank, a habitat in which HILLIS & PATTON (1982) found the "white form" to predominate. However, the mean number of growth rings ("annuli") for our sample was less than for the Texas sample and, when number of annuli was plotted against shell mass for each clam, all our values fell below the "envelope" surrounding the values that HILLIS & PATTON (1982) derived (their Figure 1) for the "white form" in Texas.

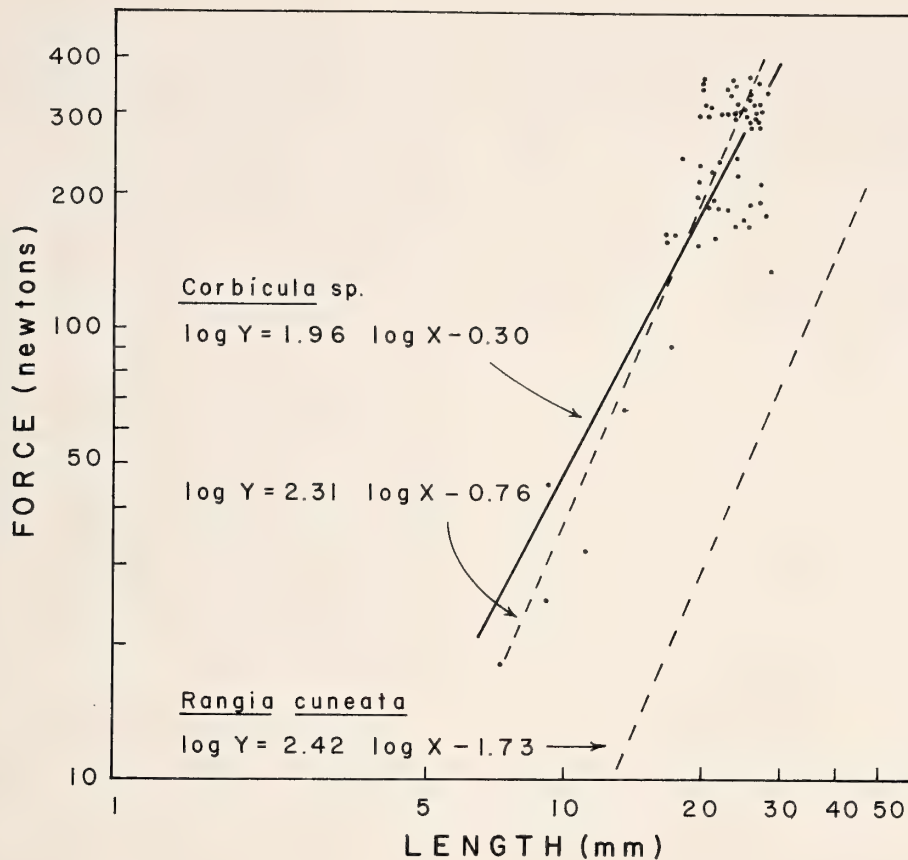


Figure 1

Predictive regression (—) and geometric mean functional regressions (-----) for shell strength of Asiatic clam (*Corbicula* sp.) and wedge clam (*Rangia cuneata*) from Maryland. Wedge clam data are from BLUNDON & KENNEDY (1982).

We agree with HILLIS & PATTON (1982) that the assignment of a species name to populations of *Corbicula* is unwarranted until conclusive taxonomic studies are performed; thus we have called our bivalves *Corbicula* sp. in this report. In referring to the reported work of others, we have kept the species names they used. Specimens from our study population have been deposited with the Smithsonian Institution's National Museum of Natural History (USNM 804414).

METHODS

To test for shell strength, we used an Instron testing machine, an industrial instrument that measures compression applied to a surface (BLUNDON & KENNEDY, 1982). Clams were crushed with a steel bar, 11 mm in diameter, which moved vertically downward at a velocity of 4 mm/s. Clams were crushed in the umbo region, parallel to the dorso-ventral axis. A chart recorder was used to record force (in

newtons) required to crack the clam shell. A 10-newton weight was used to calibrate the Instron before and during the experiment. Clams for crushing were collected from Whites Ferry and were crushed immediately upon return to the laboratory (within 2 h of collection).

RESULTS

Initially, \log_{10} force (Y) was regressed on \log_{10} length (X), length being the maximum anterior-posterior axis in mm, and a regression line ($\log Y = 1.96 \log X - 0.30$) was fitted (Figure 1). The coefficient of determination, R^2 , was equal to 0.73 ($n = 70$). Because the measurements of force and size are subject to error of measurement, a geometric mean estimate of the functional regression may be a more appropriate linear regression (RICKER, 1973). The resultant equation (Figure 1) is: $\log Y = 2.31 \log X - 0.76$. This curve is significantly different from zero ($P < 0.001$).

As a comparison with these data, the geometric mean

regression for *Rangia cuneata*, an oligohaline bivalve resident in Chesapeake Bay, is presented in Figure 1. *Rangia cuneata*, like the Asiatic clam, is a globose bivalve with a thick shell and closely fitting valves. It was the strongest bivalve we tested in our survey of shell strength of eight estuarine bivalves (BLUNDON & KENNEDY, 1982). However, the Asiatic clam had a stronger shell than did *R. cuneata* (Figure 1). The slopes of the geometric mean regression for the two species were not significantly different ($P > 0.05$), according to the test statistic of CLARKE (1980). However, the elevations of the two curves were significantly different ($P < 0.001$), as determined by Hotelling's T^2 (MORRISON, 1967).

DISCUSSION

As noted earlier, MACKIE (1978) found that the shell of *Corbicula fluminea* was the thickest of the shells of 23 species of sphaeriacean clams he studied. Neither MACKIE (1978) nor COUNTS & PREZANT (1982) present evidence that the shell of *Corbicula fluminea* is unusual in its structural material or in the arrangement of that material. In addition to shell thickness, the globose shape of the Asiatic clam, like *Rangia cuneata*, is probably an important reason for the crushing resistance being so high.

COVICH *et al.* (1981) noted that freshwater crayfish, *Procambarus clarkii*, attacked the edge of the shell of Asiatic clams with their mandibles. Repeated chipping of the shell led to eventual penetration. Such chipping away at shell edges should allow a relatively weak predator to open a strong-shelled bivalve. This chipping method was successful only with clams less than 6 mm long. Asiatic clams greater than 6 mm were successfully preyed upon by the crayfish *Cambarus bartonii* if the clams had suffered damage, such as perforations in the shell, which allowed the crayfish to reach their first walking leg into the soft clam body.

BROWN *et al.* (1979) found that a 33.7-g specimen of *Procambarus clarkii* could exert an average force of 9.9 newtons in the region of the base of the chelipeds, with force decreasing to 3.4 newtons near the tip of the chelipeds. The *P. clarkii* used by COVICH *et al.* (1981) ranged in size from 21.0–34.6 g, averaging 27.8 g. Using our geometric mean regression equation, we find that a 4-mm and 6-mm long Asiatic clam (respectively, the minimum and maximum size of undamaged prey that *P. clarkii* opened, according to COVICH *et al.*, 1981) have an average shell strength of about 4 newtons (4-mm clam) to 11 newtons (6-mm clam). Thus, if our data are transferable to southern clams, the crayfish used by COVICH *et al.* (1981) may not have been able to crush the Asiatic clams greater than 6 mm long, even if they had used their chelipeds in a crushing attempt (Covich *et al.* do not report any attempts by *P. clarkii* to use their chelae to crush shells).

Theoretically, the larger crayfish (*e.g.*, 34.6 g) could crush the smallest (4 mm) clams available, assuming that the chelae could grip the globose shell appropriately.

With regard to other sources of shell damage that might leave Asiatic clams susceptible to crayfish predation, our clams were collected from a substrate of gravel and pebbles covered with silt, with cobble stones and boulders also present. Fast river flow during floods (*e.g.*, in spring) might cause substrate movement, with tumbling of clams or rocks and with grinding and pressure on shells. Strong shell structure would seem a useful protective measure under such conditions. COVICH *et al.* (1981) found damaged (perforated) shells in a rocky region of variable water flow below a dam. We have not noted much broken or damaged shell in our monthly surveys of Asiatic clams in our collecting area; most dead shell has consisted of intact valves.

We conclude that the thickness and globose shape of the shell of the Asiatic clam, which probably accounts for its considerable strength, should provide protection from predator crushing attack, especially for larger clams. This strength may also protect the clams in situations where they, or rocks, are being tumbled about in fast-flowing waters.

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Relationship Between Beak Morphometrics and Live Wet Weight of the Giant Pacific Octopus, *Octopus dofleini martini* (Wülker)

by

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Abstract. Twelve separate beak measurements were taken on 73 different sets of beaks and a relationship was established with the live weight of *Octopus dofleini martini* (Wülker). The pigment upper-lateral-wall length best predicted the weight of the octopus after taking the natural logarithm of each measurement. Pigment lengths were found to be slightly more accurate than the corresponding total lengths. We could find no set of measurements which would permit discrimination between sexes based on beak morphometrics.

INTRODUCTION

THE HORNY MANDIBLES, called beaks, found within the buccal mass of cephalopods have received attention for a number of different reasons. There has been considerable interest in their function during feeding (ALTMAN & NIXON, 1970), the organization of their movements (BOYLE *et al.*, 1979a, b) and their potential in taxonomic work (CLARKE, 1962a, b; AKIMUSHKIN, 1965; MANGOLD & FIORONI, 1966; CLARKE & MACLEOD, 1980; IVERSON & PINKAS, 1971). Studies also indicate the possibility of using beak measurements to estimate cephalopod body size (CLARKE, 1962b; NIXON, 1969, 1973) and in the case of the squid *Illex illecebrosus* to differentiate between sexes (MERCER *et al.*, 1980).

The ability to identify cephalopods by their beaks and to estimate their size from measurements of these hard parts provides considerable opportunity to extract information from stomach analyses of marine predators. Such information includes indications of predator migratory patterns (CLARKE & STEVENS, 1974), predator diet (see, for example, PITCHER, 1981; RANDALL *et al.*, 1981), cephalopod distribution (CLARKE, 1962c), and the relative importance of cephalopods in the ecology of the oceans (CLARKE, 1977). Clarke's report of 18,000 beaks in the stomach of one sperm whale gives some impression of their importance to these marine mammals.

Much of the work on beaks has centered on various species of squids, although NIXON (1969, 1973) has car-

ried out studies on *Octopus vulgaris* beaks. No information is available on beaks of the giant Pacific octopus, *Octopus dofleini*, although a brief description is given by WINKLER & ASHLEY (1954) and PICKFORD (1964). Pickford describes possible growth lines on beaks and records rostral length indices for this species.

Octopus dofleini martini is an abundant, fast-growing form inhabiting the coastal waters of British Columbia and extending as far south as California. Its current status, as a candidate for fisheries development (HARTWICK *et al.*, 1978), means that information on its distribution, mortality and predator-prey size relationships is desirable. Since examination of beaks may provide such information, an attempt was made to measure a series of beak dimensions and to relate these to body size and sex.

MATERIALS AND METHODS

During May, 1981, to February, 1982, 73 animals (15 males, 58 females) were captured in Clayoquot Sound on the west coast of Vancouver Island, British Columbia. SCUBA was used to collect the octopuses, and the first animals encountered were captured and taken to a vessel at the surface. After draining the mantle cavities, live wet weights were taken using spring scales sensitive to 0.25 kg for animals over 3 kg and 0.025 kg for animals less than 3 kg. The entire buccal mass was then removed from the animal and stored in 10% formalin in seawater. Later, beaks were gently excised from the surrounding muscle

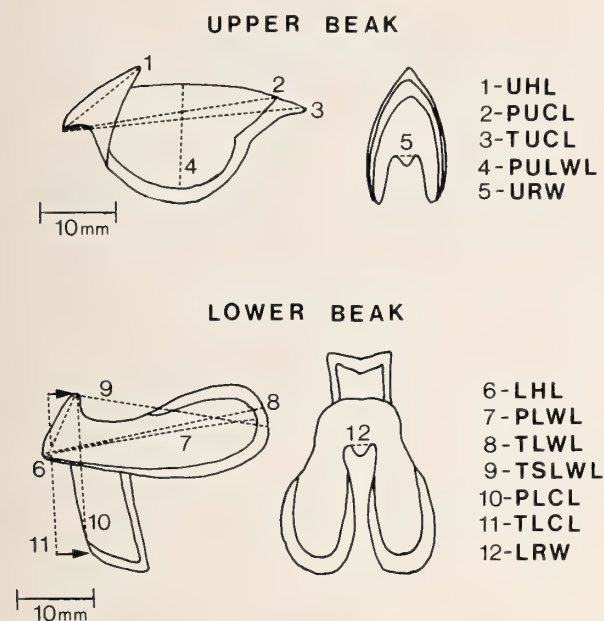


Figure 1

Measurements taken on upper and lower beaks of *Octopus dofleini*.

tissues and measured, using Vernier calipers, to the nearest 0.05 mm. Twelve measurements per beak were taken using terminology modified from CLARKE (1962b). As the octopus grows, new chitin is added to the edge of the wings, crest, and lateral wall (NIXON, 1969). This leaves a translucent margin on the edges where it has not become dark and horny. The interface of this translucent area with the pigment is used for the measurement of the pigment length. The measurements taken were: pigment upper-crest length (PUCL), pigment lower-crest length (PLCL), pigment upper-lateral-wall length (PULWL), pigment lower-wing length (PLWL), total upper-crest length (TUCL), total lower-crest length (TLCL), total lower-wing length (TLWL), total standard-lower-wing length (TSLWL), upper hood length (UHL), lower hood length (LHL), upper rostral width (URW), and lower rostral width (LRW) (Figure 1).

Analysis of the data was carried out using least-squares regression and discriminant analysis, both statistical computer package programs (MIDAS). Correlation tests were taken from SOKAL & ROHLF (1969, p. 521).

RESULTS AND DISCUSSION

In this study, we attempted to predict the live wet weight of the octopus from the beak measurements. This was chosen over other measurements, such as the dorsal mantle length, since body weight seems to be a more accurate measurement of size than length in live material (NIXON, 1968). The weight range of animals measured was from

Table 1

Regression statistics of the natural logarithm of beak measurements (mm) versus the natural logarithm of live wet weight (kg) for *Octopus dofleini* (n = 73). (r = correlation coefficient; SE = standard error of regression; m = slope; b = y-intercept.)

Measurement	r*	SE	m	b
ln PULWL	0.970	0.044	0.274	2.674
ln PLWL	0.967	0.045	0.265	2.969
ln PUCL	0.965	0.048	0.277	3.122
ln PLCL	0.959	0.050	0.268	2.710
ln TLWL	0.946	0.053	0.245	3.074
ln TSLWL	0.938	0.058	0.248	2.926
ln TUCL	0.934	0.060	0.247	3.273
ln TLCL	0.927	0.068	0.264	2.832
ln UHL	0.921	0.061	0.228	2.382
ln LHL	0.909	0.074	0.253	1.954
ln URW	0.885	0.082	0.244	1.216
ln LRW	0.784	1.131	0.261	1.059

* All r's are highly significant at the 99% confidence level.

0.95 to 22.75 kg with a mean weight of 7.64 kg. There was a non-linear increasing function of beak measurements on wet weight so the natural logarithms of both axes were taken in order to obtain a linear function. A transformation to the cube root of the live wet weight was also attempted, to test whether a better fit of the data to a line was obtained, but the fit was not as good as taking the natural logarithm of both axes.

The relationships between the twelve measurements on the upper and lower beaks may be seen in Table 1. It is apparent from this table that all the beak measurements are good predictors of octopus weight with the correlation coefficients (r) ranging from 0.784 to 0.970. Although the best measurement is the pigment upper-lateral-wall length (PULWL), shown in Figure 2, there is really very little difference among the first three measurements. All of the beak measurements in Table 1 have been grouped from the highest correlation coefficient to the lowest and this resulting hierarchy allows one to choose the best measurement that is available. A hierarchy of possible mea-

Table 2

Significance of the correlation coefficient values between corresponding pigment and total length beak measurements (Fisher's z transformation).

Comparison 1 vs. 2		n	z(1)	z(2)	P <
ln PUCL	ln TUCL	73	2.0191	1.6902	0.052
ln PLCL	ln TLCL	73	1.9345	1.6376	0.080
ln PLWL	ln TLWL	73	2.0484	1.7943	0.133

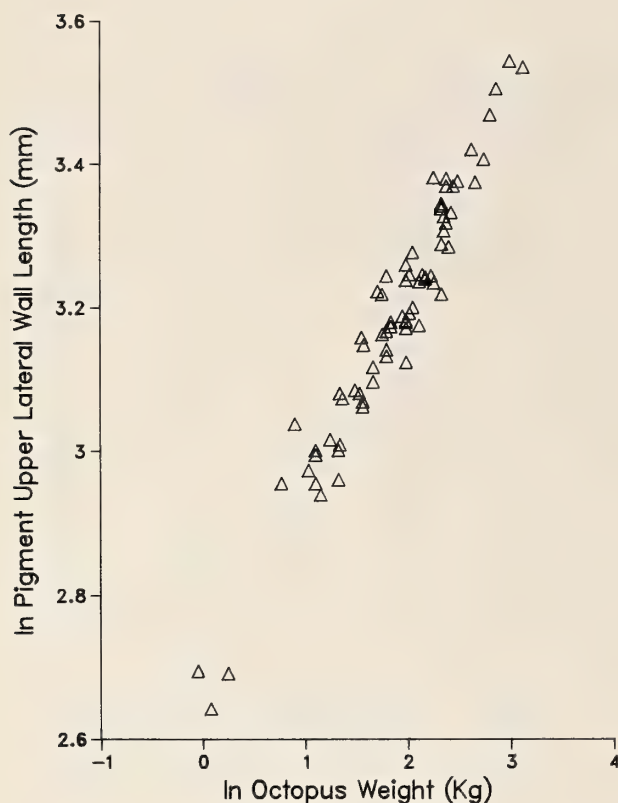


Figure 2

The relationship between pigment upper-lateral-wall length and live wet weight of *Octopus dofleini* (natural logarithms of both axes).

measurements would be advantageous if only one of the beaks was available and/or it was damaged in some way necessitating an alternate measurement.

Our results compare favorably with those of NIXON (1973) with *Octopus vulgaris*. She found that after boiling the beaks in a 5% potassium hydroxide solution to remove the surrounding muscle tissue, there was a high degree of correlation ($r = 0.97$ with $n = 77$) between the logarithm of live wet weight and the logarithm of crest length of the upper beak. It is interesting to note that the correlation coefficient for the pigment upper-crest length (PUCL) in our study is essentially the same as Nixon's with approximately the same number of samples taken, and that an upper-beak measurement is generally more accurate in predicting weight than its corresponding one on the lower beak.

In our study, essentially two types of measurements were made: pigment lengths and total lengths, although four measurements—UHL, LHL, URW, and LRW—were not readily assignable to either of these. As can be seen from Table 1, there is a distinct grouping of measurements with the pigment lengths in every case having higher correlation coefficients than the total lengths. To

determine whether a significant difference existed between these two types of measurements, Fisher's z-transformation test was carried out (Table 2). Three sets of corresponding measurements were used, and the data show that there is only a slightly significant difference between them (ranging from $P < 0.05$ to $P < 0.13$). Despite the low levels of significance, the use of pigment lengths over total lengths is warranted by the fact that often the delicate translucent edge will be destroyed if the beak is not carefully removed from the muscle tissue of the buccal mass.

Although MERCER *et al.* (1980) were able to differentiate between sexes of the squid *Illex illecebrosus* using beak morphometrics in a discriminant analysis, our attempts to find a set of beak measurements in *Octopus dofleini* which would separate sexes using this technique were unsuccessful. Although this may have been due, in part, to a small sample size of males, there was a large degree of overlap between the generated male and female discriminant values.

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Studies on the Reproductive Biology of Some Prosobranchs from the Coast of Pakistan Bordering the Northern Arabian Sea. II. Egg Capsules and Larvae of Four Species of *Thais*

by

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Abstract. Egg masses of four species of *Thais*, namely, *T. rudolphi*, *T. carinifera*, *T. bufo*, and *T. tissoti*, are reported from the coast of Pakistan for the first time. Based on the incidence of their egg capsules, the respective breeding seasons of the four species are: June to September, February to November, April to August, and March to August. The four species deposit benthic egg capsules from which free-swimming veligers are hatched. A comparative account of numbers and dimensions of capsules, number and sizes of eggs, and developmental periods of shelled larvae is presented.

INTRODUCTION

THE EGG MASSES and capsules of prosobranch mollusks, apart from the fact that they are of scientific interest in themselves, yield information about the breeding seasons of the parent species, may prove of assistance in the precise identification of closely related species, and provide larval stages and juveniles should there be a need for their commercial rearing. Although the literature in this field is vast, only the following are the major publications on the gastropods of the Arabian Sea: THORSON (1940) from the Persian Gulf; NATARAJAN (1957) from the Gulf of Mannar and Palk Bay; GOHAR & EISAWAY (1962, 1967a, b) from the Red Sea; and DESAI (1962), GANAPATI & SASTRY (1973), RAMAMOORTHY & NATARAJAN (1973), and KASINATHAN *et al.* (1974) from different parts of the Indian coast. No information is available on the egg masses and larval development of marine gastropods from the coast of Pakistan bordering the northern Arabian Sea. It was in view of this paucity of information that a project was initiated in 1976 at the Institute of Marine Biology, University of Karachi, to study the same. Observations on the juveniles of the gastropod *Planaxis sulcatus* from the coast of Karachi have already been published (BARKATI & AHMED, 1982). The present report on four species of *Thais* is the second in the series.

MATERIAL AND METHODS

In order to collect egg masses and capsules of local gastropods, regular biweekly visits were made during the period June, 1976, to July, 1977, to Buleji, which is a rocky and partly sandy-cum-muddy beach about 18 km northwest of Karachi. Egg capsules were also collected rather irregularly from some other beaches in the Karachi area, namely, Manora Island, Keamari Seawall, Paradise Point, and Korangi Creek, and from Gawader and Jiwani on the Mekran coast, about 600 km northwest of Karachi. Some egg capsules had been collected prior to June, 1976, and others after July, 1977. Except for a couple of rainy months in summer the salinity at all these sites is high, ranging from 36-40‰. In most of the cases the spawning female snails were present near their egg masses. It was difficult to ascertain the number of egg capsules spawned by individual snails since the capsules are laid together. During the study, therefore, only representative samples of egg capsules were collected although some of these consisted of the entire lots of capsules spawned by individual snails.

Attempts to spawn specimens of the different species of *Thais* in the laboratory in limited quantities of water did not succeed. The egg capsules, and the larvae hatching from these, were maintained in filtered and aerated sea

water in 1600-ml glass bowls. They were fixed in 5% formalin and then preserved in 70% ethanol for subsequent study. Measurements of the size of capsules, eggs, and larvae were made with an ocular micrometer on a microscope. Illustrations were prepared with a camera lucida.

OBSERVATIONS

Breeding Season

The four species of *Thais* investigated occur near the low and mid-tidal zones of the rocky beaches of the coast of Pakistan. The number of egg masses of four species collected from different localities is given in Table 1. It is apparent from this table that *T. rudolphi* (Lamarck) spawns from June to September, *T. tissoti* (Petit) from March to August, and *T. bufo* (Lamarck) from April to August. An egg mass of *T. carinifera* (Lamarck) was taken at station 45 (63°46'N latitude) along the Mekran coast on March 1, 1977, in a purse seine haul of the Norwegian Fisheries Research Vessel "Dr. Fridtjof Nansen" (egg capsules of this species in THORSON's [1940] collection from the Persian Gulf were obtained from a depth of 11–22 m). Since some of the capsules in this egg mass were of purple color they must have been spawned in February. Recently, an egg mass of *T. carinifera* was also collected from Port Qasim, about 30 km southeast of Karachi. The spawning season of *T. carinifera* on the coast of Pakistan, therefore, seems to extend from February to November.

Characteristics of Egg Capsules, Eggs, and Larvae

Egg capsules of *T. rudolphi* (Figure 1A, B), like those of other species of *Thais*, are creamy white in color when deposited and become dark gray with the advancement of embryonic development. A change in color from yellow to gray was also observed by NATARAJAN (1957) in *T. bufo*. The capsules are deposited in clusters of several irregular, short rows imparting a circular shape to the egg mass in general. There is always one layer of capsules the basal plates of which unite to form a common basal membrane that is firmly glued to the substratum. Each capsule has translucent, tough leathery walls. An aperture for the release of larvae, 0.32 mm in diameter, is present slightly off center on the flattened, apical surface of each capsule and is covered with a transparent membrane which ruptures at the time of larval hatching. Dimensions of capsules, eggs, and larvae of this species are given in Table 2. The larvae just after hatching (Figure 1C, D) possessed shell lengths of 211 to 251 μm and widths of 171 to 182 μm . They swam actively and gathered near the walls of the glass bowls. Their shells consisted of one and a half whorls. They measured 353 to 376 μm in height and 274 to 285 μm in width 36 h after hatching.

The egg mass of *T. carinifera* consists of closely spaced, stalkless, somewhat curved and thin tubular capsules that

Table 1

The incidence of egg masses of four species of *Thais* on the coast of Pakistan. Exposure of shore abbreviated as: Exposed, E; Protected, P; Semi-exposed, SE; Subtidal, ST.

Locality	Exposure	Date	Year	Egg masses
<i>T. rudolphi</i>				
Manora Island	E	June 9	1970	Many
Buleji	E	June 15	1976	1
Manora Island	E	June 16	1976	2
Buleji	E	July 2	1976	2
Buleji	E	July 3	1977	4
Buleji	E	August 13	1976	1
Paradise Point	E	August 26	1975	1
Buleji	E	September 8	1975	1
Buleji	E	September 9	1976	2
Paradise Point	E	September 9	1976	1
<i>T. carinifera</i>				
Mekran Coast	ST	March 1	1977	1
Jiwani	SE	April 29	1979	3
Korangi Creek	P	April 30	1978	1
Native Jetty	P	May	1972	Many
Buleji	E	June 14	1980	1
Keamari Seawall	P	August 1	1976	3
Port Qasim	P	November 1	1982	1
<i>T. tissoti</i>				
Sandspit Bridge	P	March 16	1979	1
Jiwani	SE	April 29	1979	2
Korangi Creek	P	April 30	1978	1
Buleji	SE	June 4	1980	1
Manora Island	E	June 9	1970	Many
Keamari Seawall	P	August 1	1976	1
Korangi Creek	P	August 21	1977	Many
<i>T. bufo</i>				
Jiwani	SE	April 29	1979	1
Keamari Seawall	P	May	1975	3
Keamari Seawall	P	May 18	1976	1
Manora Island	E	June 9	1970	Many
Keamari Seawall	P	June 13	1975	1
Manora Island	E	June 13	1979	1
Keamari Seawall	P	August 1	1976	1

have very smooth translucent walls without any ridges (Figure 2A, B). They are of uniform width but taper at the apex to form a nipple-like structure. The apex functions as an operculum which is shed at the time of hatching so as to provide an exit for the larvae. This aperture is 0.4 mm in diameter. Dimensions of capsules, eggs, and larvae of this species are given in Table 2. The larvae 12 h after hatching (Figure 2C, D) measured $388 \times 295 \mu\text{m}$. Their shell walls were smooth and transparent and consisted of one and a half whorls. They attained a size of $401 \times 301 \mu\text{m}$ (Figure 2E) after 36 h of development. Very few larvae survived in the laboratory for 60 h without food. The egg mass of *T. carinifera* was described

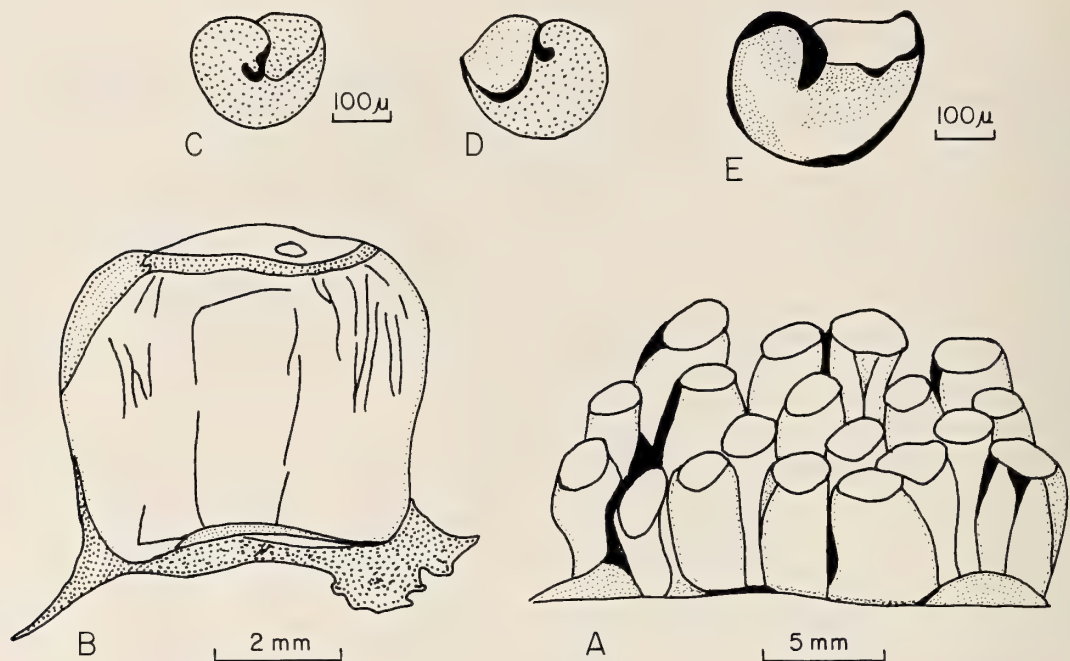


Figure 1

Thais rudolphii: A. dorsolateral view of a portion of an egg mass; B. dorsolateral view of an egg capsule; C. ventral view of a larval shell just after hatching; D. dorsal view of the same; E. ventral view of 36-h larval shell.

earlier by ANNANDALE & KEMP (1916) from Chilka Lake, India, and by THORSON (1940) from the Red Sea. NATARAJAN (1957) also described an egg mass that closely fits the above description but he was not able to assign it to any species.

Egg capsules of *T. tissoti* are stalkless (Figure 3A, B) and attach themselves to the substratum by their basal plates, which unite to form a basal membrane. The capsules are smaller than those of *T. carinifera*. They are cylindrical, somewhat broader in the middle, taper at both ends, and curve on one side. Their walls are smooth and without ridges. A preformed aperture for the release of larvae does not exist but the apex of the capsule sheds off at the time of hatching. The part shed measures 0.72×0.32 mm across. Dimensions of capsules, eggs, and larvae of this species are given in Table 2. The larval shell (Figure 3C) soon after hatching consists of one and a half whorls. Changes in the size of the larval shell of this species with time are shown in Table 3. The larvae thrived in the laboratory without food for about nine days but showed very little increase in shell dimensions after 84 h. The maximum shell dimensions recorded were: height 467 μ m and width 456 μ m.

The capsules of *T. bufo* (Figure 4A, B, C) have smooth and very thick walls, are tubular in shape, and have long thin stalks which unite at the base and are glued to the substratum. The proximal end of the capsules is swollen

and carries a rounded aperture for the exit of larvae. The aperture measures 0.49 to 0.58 mm in diameter and is covered by a thin membrane. The larvae (Figure 4D, E) hatch from the capsules as free-swimming veligers. Their dimensions appear in Table 2.

The egg mass of *T. bufo* was earlier described from south Indian waters by Gravely (1942, in NATARAJAN, 1957), Chari (1950, in NATARAJAN, 1957) and by NATARAJAN (1957) and the above account describes it closely.

An egg mass was collected from the bottom of a crevice of a steep rocky ledge at Paradise Point that might be from a fifth species of *Thais* (or another muricid). This ball-like egg mass measured 2.4×2.2 cm across and consisted of two layers of low rounded and irregularly shaped capsules which were stalkless, with their basal plates united to form a common membrane.

DISCUSSION

Observations made during the present study show that three of the four species of *Thais* examined, namely, *T. bufo*, *T. tissoti*, and *T. carinifera*, spawn for about six to seven months in the spring and summer during the period February to August, whereas *T. rudolphii* has the shortest spawning season of four months, restricted to the summer months of June to September. There is evidence that spawning in at least two of these species, namely, *T. bufo*

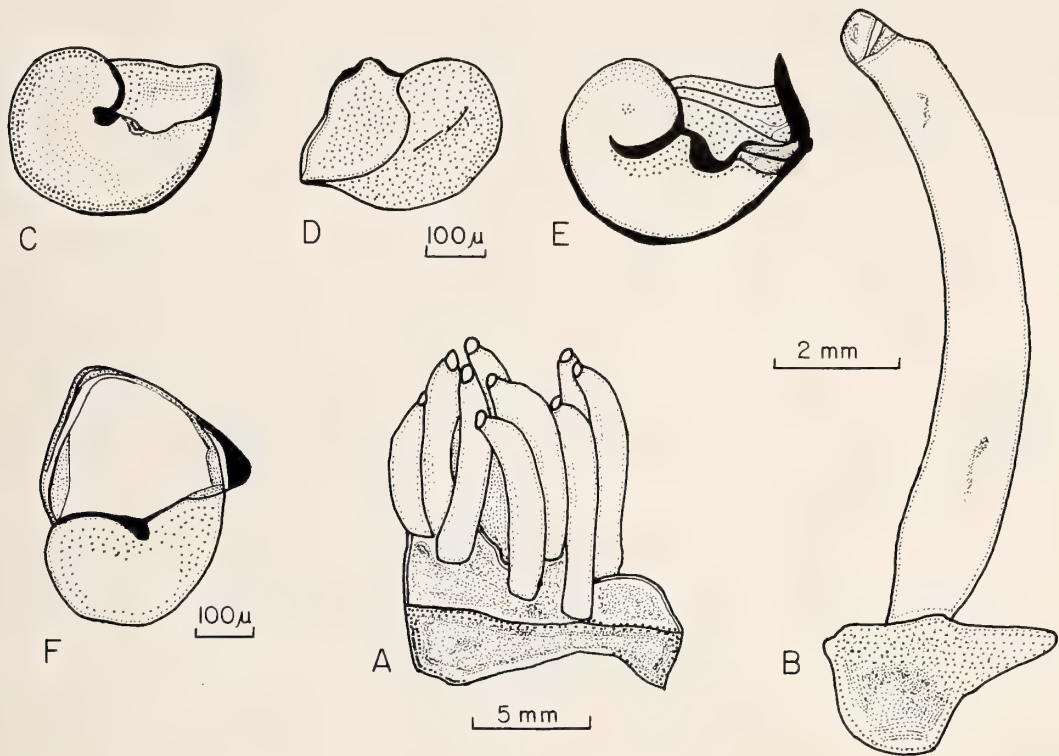


Figure 2

Thais carinifera: A. dorsolateral view of a portion of an egg mass; B. lateral view of a single egg capsule; C. ventral view of veliger shell 12 h after hatching; D. dorsal view of the same; E. ventral view of larval shell 36 h after hatching; F. front view of the same.

Table 2

A comparative account of the characteristics of egg capsules, eggs, and larvae of four species of *Thais*. Data are presented as averages with the range of values given in parentheses.

Characteristics	<i>T. rudolphi</i>	<i>T. carinifera</i>	<i>T. tissoti</i>	<i>T. bufo</i>
Approximate size of females (cm)	6.8 (4.0–8.0)	4.6 (3.5–6.0)	3.2 (2.5–4.0)	5.8 (4.0–7.0)
Number of egg capsules per mass	170 (97–257)	247 (220–268)	257 (255–295)	80 (65–92)
Capsule height (mm)	4.6 (3.8–5.0)	9.1 (8.0–10.5)	4.2 (4.0–4.4)	7.9 (7.2–9.0)
Capsule width (mm)	5.3 (4.0–6.1)	1.3 (1.2–1.5)	1.2 (1.1–1.2)	2.0 (1.8–2.5)
Number of eggs per capsule	1094 (813–1422)	140 (120–160)	37 (25–40)	228 (183–268)
Egg diameter (μm)	142 (137–148)	230 (216–250)	215 (200–250)	252 (198–350)
Hatching time (days)	17 (16–18)	19 (18–20)	19 (18–20)	20 (18–22)
Larval size at hatching (L × W) (μm)	224 × 173	340 × 276	231 × 198	322 × 255

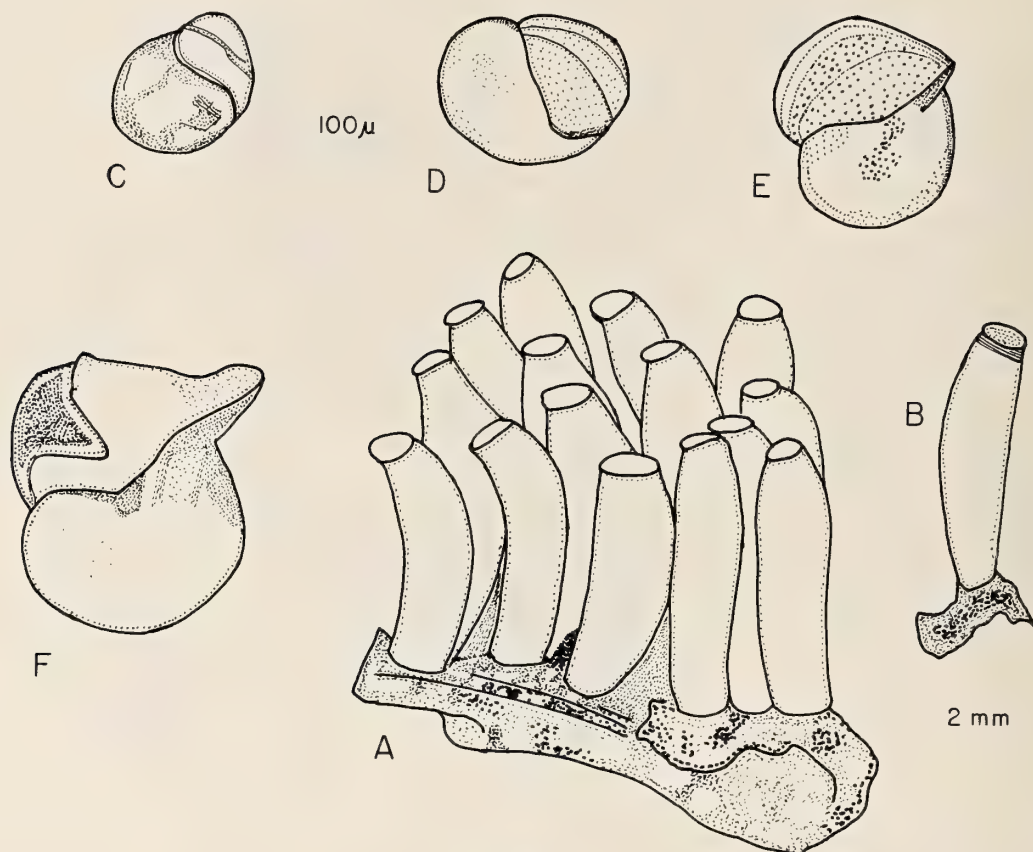


Figure 3

Thais tissoti: A. dorsolateral view of a portion of an egg mass; B. lateral view of a single egg capsule; C. ventral view of veliger shell taken out of a capsule; D. ventral view of 24-h veliger shell; E. front view of 84-h veliger shell; F. front view of larval shell 13 days after hatching.

and *T. carinifera*, may commence slightly earlier on the coast of Mekran than on the coast of Karachi. Be as it may, spawning in the four species of *Thais* seems to occur with the rising temperatures of spring and summer when a lowering of salinity may also occur due to the southwest monsoon rains (see AHMED, 1980).

The study shows that *T. rudolphi* produces the highest

numbers of eggs per capsule, and *T. carinifera*, *T. bufo*, and *T. tissoti* follow it in that order. Survival of the brood in the natural environment seems to be in the same proportion, since *T. rudolphi* is the most abundant species of *Thais* on the coast of Karachi followed by *T. carinifera*. *Thais rudolphi* has not been recorded from Gawader and Jiwani on the Mekran coast where *T. carinifera* does occur (AHMED *et al.*, in press). *Thais rudolphi*, the species with the highest fecundity, also has been found in the present study to have eggs and larvae of the smallest size among the four species. Larvae of the four species spend about 16–22 days within egg capsules but those of *T. rudolphi* hatch the earliest.

Species of *Thais* are known to display two types of larval development. The first is the indirect development in which pelagic planktrophic or lecithotrophic veliger larvae hatch from egg capsules. The second is direct or non-pelagic development in which crawling miniature snails emerge from egg capsules and where a planktonic stage is missing. The four species of *Thais* examined in the present study also possess indirect development, which

Table 3

Changes in the size of the larval shell of *Thais tissoti*. Egg size is 200–225 μm .

	Just after hatching	Size (μm)				
		12 h	36 h	60 h	84 h	9 d
Length	231	281	313	338	385	460
Width	198	229	232	269	302	442

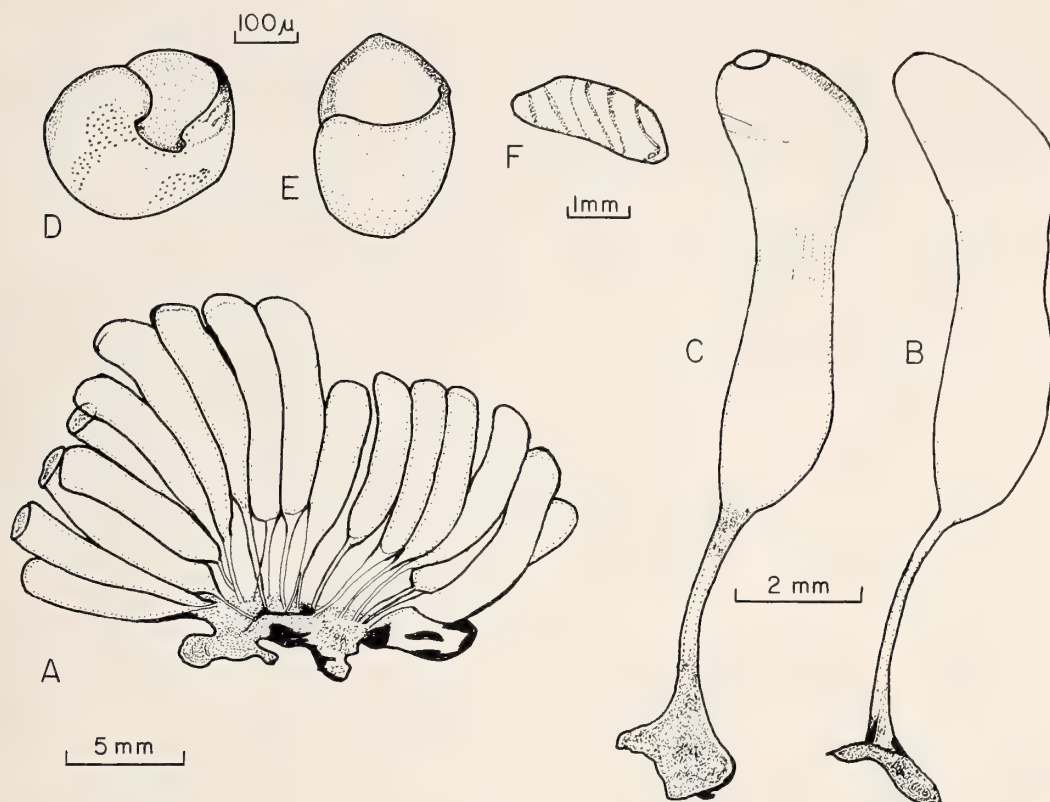


Figure 4

Thais bufo: A. lateral view of an egg mass; B. and C. dorsal and ventral views of egg capsules; D. ventral view of a veliger shell taken out of a capsule just before hatching; E. front view of the same; F. tip of an egg capsule.

is shown by a majority of the species of *Thais* studied so far in different parts of the world: for instance, *T. carinifera* (THORSON, 1940); *T. fasciata* (LEBOUR, 1945); *T. coronata* (KNUDSEN, 1950); *T. bufo*, *T. tissoti*, and three unidentified species of *Thais* from India (NATARAJAN, 1957); and *T. haemastoma* (D'ASARO, 1970). Species that show direct development are *T. hippocastaneum* (THORSON, 1940), *T. lapillus* (see THORSON, 1940), *T. lamellosa*, *T. emarginata* (= *T. lima*), and *T. canaliculata* (see AHMED & SPARKS, 1970), and *T. emarginata* (LEBOEUF, 1972; SPIGHT, 1976). There are, however, instances where members of the same species of *Thais* may behave differently under different environmental conditions. For instance, *T. haemastoma* is believed to have pelagic larval development in Louisiana but direct development in the West Indies (see THORSON, 1950; NATARAJAN, 1957). LYONS & SPIGHT (1973) have considered the members of the Muricacea as sufficiently variable that geographically separated species may develop according to the local conditions. We wish to point out here that some workers feel that the above reference to direct development in the West Indian species of *Thais* is based on misinformation and should not be attributed to either Thorson or Natarajan.

It is generally believed that species of prosobranch mollusks occurring in cold waters of higher latitudes show direct development but those occurring in warm tropical and subtropical latitudes possess pelagic indirect development (THORSON, 1950). However, MILEIKOVSKY (1971) pointed out, as an exception to Thorson's generalization, that pelagic development is not altogether absent in colder waters of higher latitudes and that an occasional species may display such a developmental pattern. Also as an exception can be mentioned the case of the gastropod *Planaxis sulcatus* which shows direct development on the coast of Karachi, a subtropical locality (BARKATI & AHMED, 1982).

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Comparison of Northern and Southern Populations of *Epitonium tinctum* (Carpenter, 1864) on the California Coast

by

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Abstract. *Epitonium tinctum* (Carpenter, 1864) was collected for several years from Bodega Head to the north and from Carpinteria Beach to the south of Point Conception, California. Northern populations contained longer shells than southern populations. Northern snails became sexually mature and changed sex at a larger size than southern snails. There were no distinguishable differences in the weight and width of specimens between northern and southern snails of similar length. Variation in shell shape (squat versus elongate) between populations did not exceed variation within each population. Shell length and the number of body whorls overlapped substantially between the two sites. The size and abundance of snails collected monthly fluctuated more throughout the year in the northern population than in the southern population.

INTRODUCTION

ALONG THE WEST coast of North America the wentletrap *Epitonium* (= *Nitidiscala*) *tinctum* is found intertidally in association with the aggregate or clonal anemone *Anthopleura elegantissima* (Brandt, 1835). *Epitonium tinctum* ranges from Magdalena Bay, Baja California to Forrester Island, Alaska (DUSHANE, 1979). As protandric hermaphrodites, the snails mature first as males, then, at a larger size they change sex and function as females (BULNHEIM, 1968; BREYER, 1982). Females produce a number of sand-encrusted egg cases which are strung together with a strong elastic mucous thread attached to the substrate or to the shell. When exposed at low tide, snails bury themselves in the sand between anemones and are often aggregated around a cluster of egg cases. When submerged during high-tide periods the snails become active and feed on the expanded tentacles of the anemones (HOCHBERG, 1971; SMITH, 1977; BREYER, 1982). In order to feed, the snails evert an acrembolic proboscis and either

slip the distal end over a tentacle tip or attach it at some point along the length of the tentacle. Jaws and radula are used to sever a portion of the tentacle which is then ingested upon retraction of the proboscis (RESCH, 1972).

The shell of *Epitonium tinctum* can grow to over 10 mm in length. It has three nuclear whorls and up to 8 post-nuclear whorls with about 12 thin axial costae continuous from whorl to whorl. STRONG (1941) examined shells from north and south of Point Conception, California, and noted that northern specimens were longer and appeared to be heavier and broader than southern individuals. He suggested the subspecific name of *subcoronatum* for the northern form. Although DUSHANE (1979) described similar differences, she did not recognize the subspecies *subcoronatum* because radulae from northern and southern snails were indistinguishable.

Individuals of populations living in food-rich environments or in warm climates may be expected to grow faster than those living in more severe environments. This faster

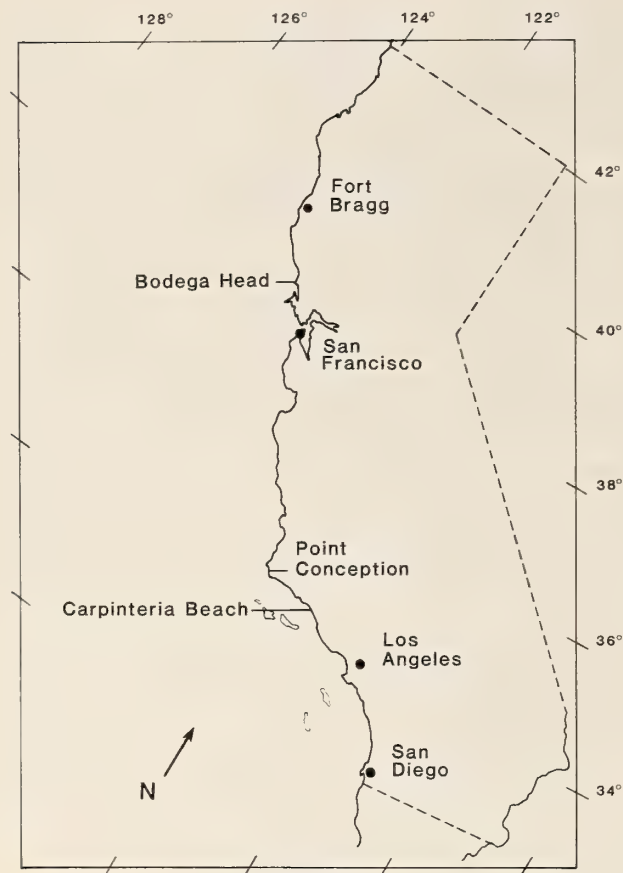


Figure 1

Map of California showing two study sites located north (Bodega Head) and south (Carpinteria Beach) of Point Conception.

growth may lead to an altered size at maturity and perhaps an important difference in generation time. In the present work we document differences within and between populations of *Epitonium tinctum* to the north (Bodega Head) and to the south (Carpinteria Beach) of Point Conception, California (Figure 1). Providing the major basis for comparison are shell parameters, which include: length, width, weight, and number of whorls and costae. Distinct population modes were computed from measurements of shell length. The mean minimum size at onset of sexual maturity and sex change were calculated from lengths of juveniles, males, and females. Additionally, fluctuations in size and abundance were noted monthly from July, 1977, to July, 1979, for populations at Bodega Head, and from July, 1978, to June, 1980, for populations at Carpinteria Beach.

MATERIALS AND METHODS

Collection Sites

The northern collecting site was in Horseshoe Cove located on the exposed outer coast of Bodega Head, So-

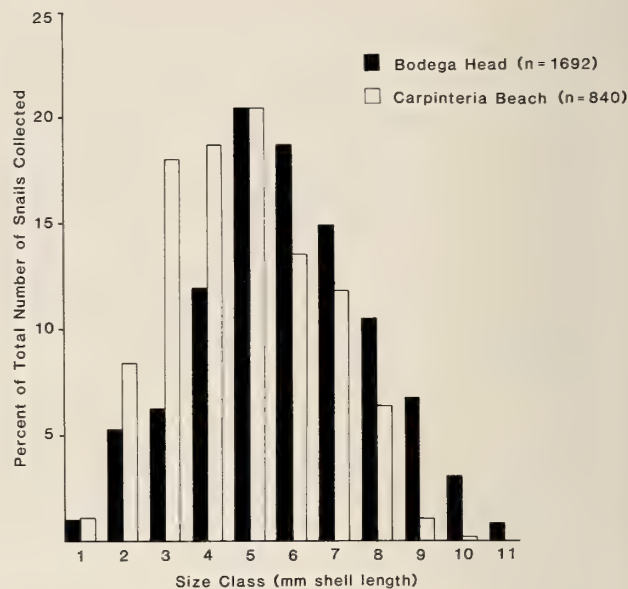


Figure 2

Comparison of *E. tinctum* shell length and the percentage of total number of snails collected from 1977 to 1980.

noma County, California. In a protected area on the northern side of the cove, a 3-m-wide surge channel located about 10 m from shore is bordered on one side by a cliff. The channel is parallel to the cliff for about 15 m until its mouth opens toward the west. Wave disturbance in this channel is reduced, not only because waves break to the south, but also because it is protected by an extensive rock shelf. At this site clones of *Anthopleura elegantissima* cover extensive areas on the sides and bottom of the channel. In the summer and fall, when wave action is reduced, the sand between the anemones is fine grained and at least 10 mm deep. During the winter, when wave action is heaviest, the amount of fine sand between the anemones is reduced, disappears altogether, or is replaced by coarser sand. Snails were collected from the anemone beds on both sides of the channel.

The rocky reef area at Carpinteria Beach State Park, Santa Barbara County, California was the southern collecting site. Carpinteria Beach, like much of the southern California coastline south of Point Conception, is characterized by sandy beaches interrupted by intermittent rocky outcrops or headlands. The Carpinteria Beach site consists of a sandy beach extending out from the cliff about 100 m to where the first rock outcrop begins. In the mid-intertidal region of the rocky reef both clonal and solitary *Anthopleura elegantissima* are present. *Epitonium tinctum* is most often found in protected areas on these rocks in sand which accumulates within pockets between clonal anemones and beneath the algal cover of *Ulva lobata* (Kützinger, 1849) and *Gigartina canaliculata* (Harvey, 1841).

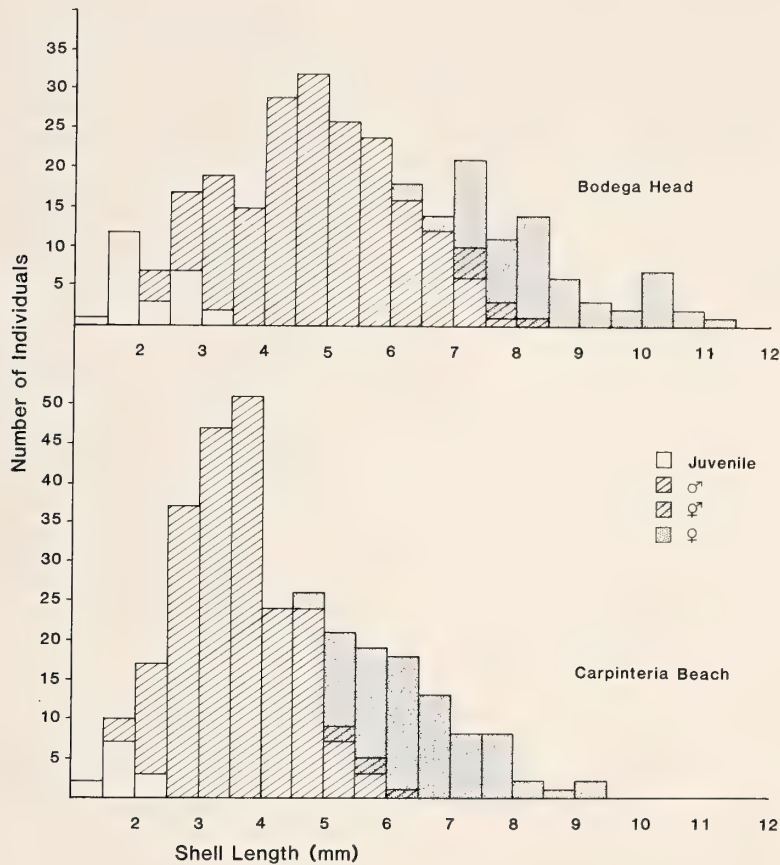


Figure 3

Comparison of *E. tinctorum* shell length versus the number of juveniles, males, and females in each population. Snails in transition from male to female (possessing both spermatzeugmata and ova) are also indicated.

Although this area receives gentle surf year around, a perceptible change occurs in the structure of the beach between summer and winter. In summer, a sand bar fills in the area between the shore and the first rock outcrop. Sand, several centimeters in depth, fills in the crevices between clonal anemones and covers many of the solitary anemones, which are primarily located lower in the intertidal. Algae flourish during this time and cover extensive surfaces of rocks. During winter storms much of the sand cover is removed from between the clonal anemones and the algal cover on the rocks is reduced.

Methods

Epitonium tinctorum was collected approximately monthly at low tide from each site; from July, 1977, to June, 1979, at Bodega Head and from July, 1978, to June, 1980, at Carpinteria Beach. Additional collections were made in 1980 and 1981 at both locations. Snails were collected by carefully searching among aggregations of

Anthopleura elegantissima in an area approximately 3 m² for 30 minutes. Similar areas, exposed at mean lower low water, were used for repeated collections at each site. Snails were located by visually scanning the area or by lightly stroking the anemones with fingertips. Pressure on the anemone body caused the release of a small amount of fluid which washed over the anemone bed and removed some sand and debris. When the tip of a snail or a clump of eggs was spotted it was carefully removed by hand. Often a mucoid thread was attached from the snail or eggs being removed to other snails and eggs in an aggregation. Care was taken to remove all snails and eggs in a particular aggregation before searching for additional snails.

Lengths and widths of snails were measured using a variety of dissecting microscopes with calibrated ocular micrometers. The number of post-nuclear whorls was determined by placing the shell with the operculum facing upward and counting from the largest body whorl to the smooth nuclear whorls. Axial costae were counted from the first costa behind the outer lip, around the body whorl,

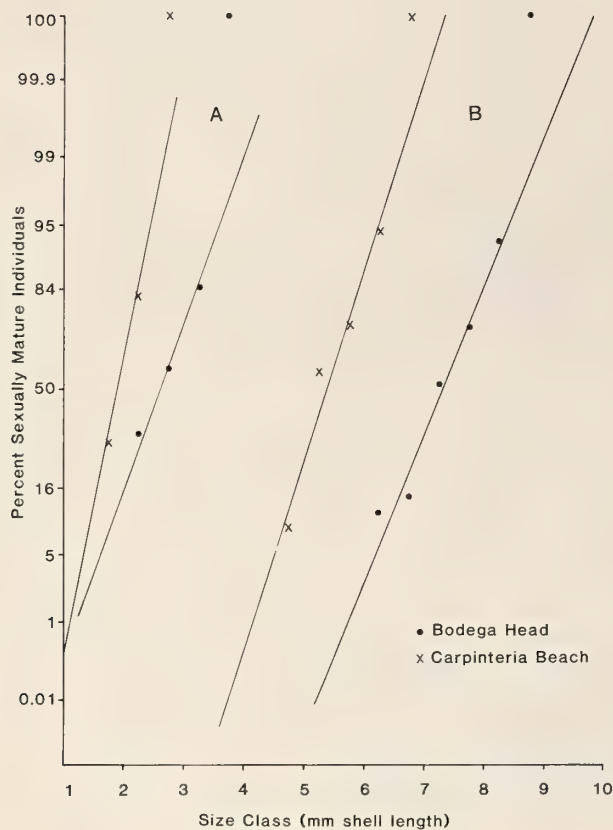


Figure 4

Mean minimum size of *E. tinctum* at onset of sexual maturity. A. Males replaced juvenile snails at an average length of 2.6 mm in Bodega Head and 1.9 mm in Carpinteria Beach. B. Females replaced males at an average shell length of 7.3 mm in Bodega Head and 5.4 mm in Carpinteria Beach. No significance test was run between sets of lines; an appropriate test is not yet in print (Wenner, in preparation).

to the point where the first costa met the costa directly above it. Weights (to 0.1 mg) were obtained on a Mettler balance from animals and shells originally preserved in 50% isopropyl alcohol, which were removed from the alcohol and allowed to air dry 24 hours at room temperature before weighing.

To determine sex, snails preserved in 70% ETOH or 50% isopropyl alcohol were first measured and then placed in a vial filled with Bouin's solution for 24 hours to dissolve their shells. Individuals were then examined with a dissecting microscope at approximately 50X. Males were recognized by the presence of spermatzeugmata, which were clearly visible as very white, almost iridescent strands densely packed in the gonad especially to the right of the stomach. Females were distinguished by the absence of spermatzeugmata and the presence of oocytes and ova. Several snails, termed hermaphroditic, were characterized

by having proximally located spermatzeugmata and distally located oocytes and ova in their gonads.

Probability Paper Analysis of Polymodal Frequency Distributions

The technique of plotting cumulative normal distributions on probability graph paper, first described by HARDING (1949), with methodology presented by CASSIE (1950), is a valuable graphical method with which to analyze bimodal or polymodal size-frequency distributions in a population. In a polymodal size-frequency sample, individual modes may be expanded and the mean and standard deviation calculated from each mode (see CASSIE, 1954, for method). If modes are compared from two or more populations, subtle differences may be distinguished. Probability paper analysis has been utilized to compare sex ratios and size in crustacean populations (WENNER, 1972) and to define and compare the mean minimum size at onset of sexual maturity in populations of the sand crab *Emerita analoga* (Stimpson, 1857) from different locations (WENNER *et al.*, 1974).

RESULTS

A compilation of size-frequency data for all snails collected and measured over a two-year period in Bodega Head and Carpinteria Beach is presented in a histogram (Figure 2). From these data a polymodal analysis of each population was calculated by the use of probability graph paper. That analysis indicated larger snails were more prevalent at the northern site than at the southern site. The modes that appear in each population were then expanded, also by the use of probability paper. Three distinct modes were calculated for each population consisting of small, medium, and large snails. For Bodega Head these values were, respectively, as follows: $\bar{x} = 2.20 \pm 0.55$ mm, $n = 152$; $\bar{x} = 5.40 \pm 1.20$ mm, $n = 1134$; $\bar{x} = 8.35 \pm 1.15$ mm, $n = 406$. For Carpinteria Beach values were, respectively: $\bar{x} = 2.65 \pm 0.77$ mm, $n = 193$; $\bar{x} = 4.75 \pm 0.90$ mm, $n = 487$; $\bar{x} = 7.20 \pm 0.90$ mm, $n = 160$. Since these snails are protandric hermaphrodites, changing from juveniles to males and then from males to females as they grow, the modes that appear possibly represent the juveniles, males, and females in each population.

More than 600 snails were examined for the presence or absence of spermatzeugmata during spring and fall (Figure 3). The size at which these protandric hermaphrodites became sexually mature and changed sex was greater in the northern population than in the southern population. In the transition from male to female in each population, snails were occasionally found with both spermatzeugmata and ova present. The data for transition of juveniles to males and males to females were plotted on probability paper (Figure 4) and the mean minimum size was calculated (*e.g.*, WENNER *et al.*, 1974). The mean size of females was larger at Bodega Head (7.3 mm) than at

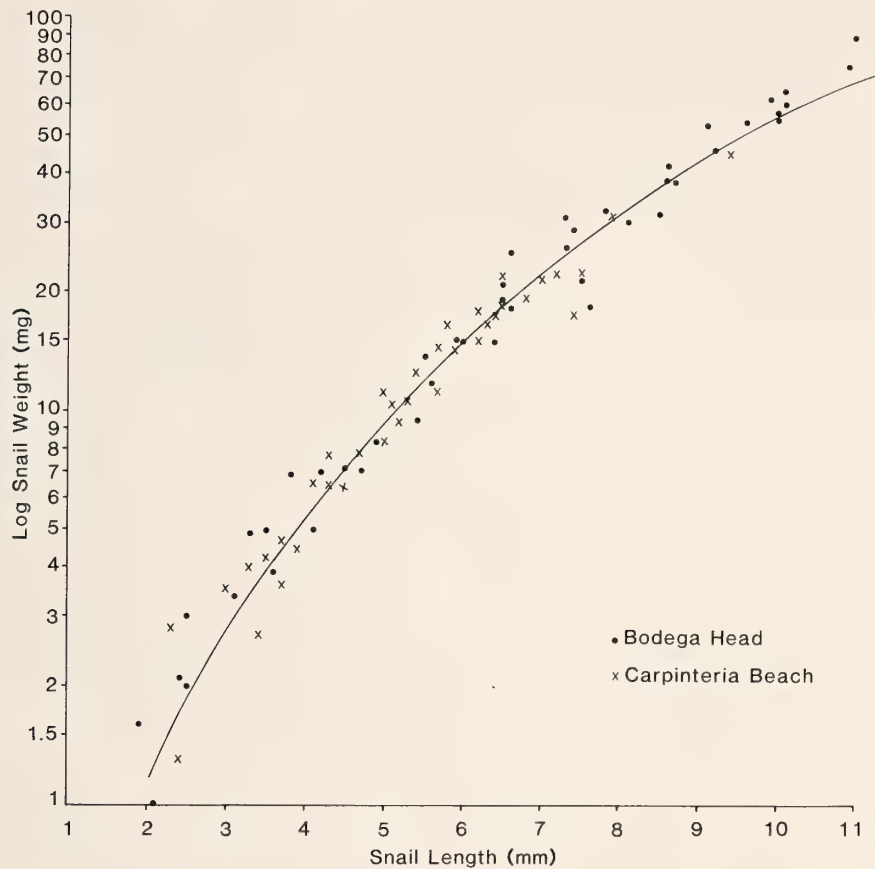


Figure 5

Comparison of *E. tinctorum* length versus weight. A complete overlap existed between sets of points, so only one curve was fitted (by inspection).

Carpinteria Beach (5.4 mm). The mean size of juveniles was also larger at Bodega Head (2.6 mm) than at Carpinteria Beach (1.9 mm).

The weights of snails (from 1.7 to 91.3 mg) in each population were obtained for snails ranging in length from 1.9 to 11.0 mm (Figure 5). The results revealed little variation in weight of snails at the same length between populations. The width of snails relative to shell length from both populations varied somewhat (Figure 6). We observed that some snails within each population appeared to have either a more squat or more elongate shell shape than the others. Although the range of variation within each population was notable, regression lines did not differ significantly between northern and southern populations. Snails of similar lengths varied considerably in number of body whorls (Figure 7), but did not differ appreciably between populations. The number of axial costae on the largest body whorl of shells from both locations ranged between 11 and 14, which agreed with DUSHANE's (1979) findings.

The size and abundance (Figure 8) of *Epitonium tinctorum* collected monthly at Bodega Head fluctuated more than in similar collections from Carpinteria Beach. Small snails (less than 3 mm) were found occasionally throughout the year at Bodega Head; however, they were most common from late winter to early summer. In 1978 many small snails were found in March and April; in 1979 few small snails were found until June; in 1980 many small snails were found in January. Every year during the summer and early fall, snails were common. In 1978 the mean shell length increased every month during this period. In the fall large females (longer than 8 mm) were most common, and particularly large clusters of egg cases associated with large aggregations of snails were found (Figure 9A). In the late fall and early winter the abundance of snails declined. Snail abundance decreased from December, 1977, to February, 1978, and from February to May, 1979. Snails remained rare until an influx of small snails appeared.

No clear annual pattern was shown at Carpinteria

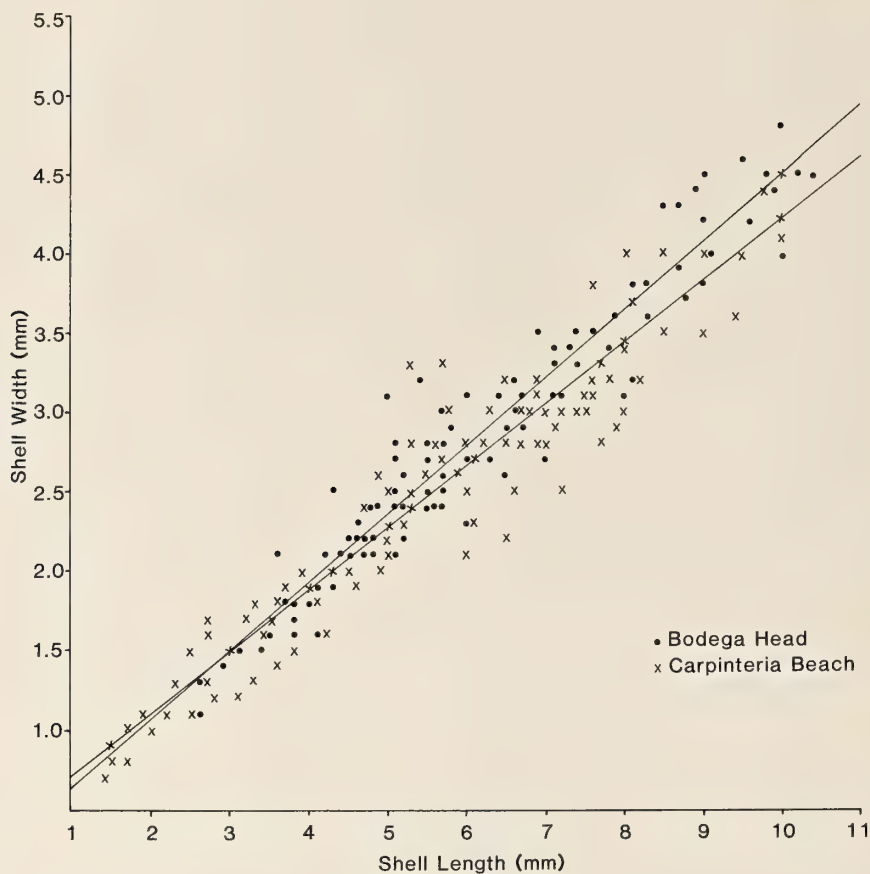


Figure 6

Comparison of *E. tinctorum* length versus width. The slopes of the lines were not significantly different ($P > 0.01$). The regression for Bodega Head was $y = 0.22 + 0.43x$ ($n = 95$) and Carpinteria Beach was $y = 0.33 + 0.39x$ ($n = 94$).

Beach for size or abundance of snails collected from July, 1978, to June, 1980. The mean snail length (4.5 to 6.0 mm) remained fairly constant through time. Newly settled snails (less than 3 mm in length) occurred commonly at all seasons. The largest individuals were observed sporadically throughout the year. Egg masses were recorded in the field in all collections in equal abundance. Snails with eggs most commonly occurred as individuals or in small groups (2–4 individuals) with few egg capsules per egg mass (less than 50 to about 500). Larger snail groups (10–15 individuals) and large egg masses (1000–5000 eggs) occurred without respect to season (Figure 9B). During the winter of 1981, severe storms washed away large amounts of sand from Carpinteria beaches. It was difficult to cross on foot from the cliff to the first rock outcrop, because of the diminished sand coupled with large waves. In February, 1981, the population of snails was greatly reduced. An influx of small snails (mean length 3.5 mm)

was noticed in the spring (April, 1981). A population fluctuation occurred at Carpinteria Beach that year similar to fluctuations observed at the Bodega Head site.

DISCUSSION

Our results support the literature on physiological variation in intertidal molluscs summarized by NEWELL (1964). He concluded that northern species generally attain a larger final size than southern ones. WEYMOUTH *et al.* (1931) studied the razor clam *Siliqua patula* (Dixon, 1789), and concluded that growth in southern localities was initially more rapid, but less sustained and hence led to smaller total lengths. There are several reasons why snails may grow larger at higher latitudes. Higher latitudes generally imply a decrease in temperature coupled with an increase in environmental stresses. CHOW (1975) concluded that the largest *Littorina scutulata* (Gould, 1849) had

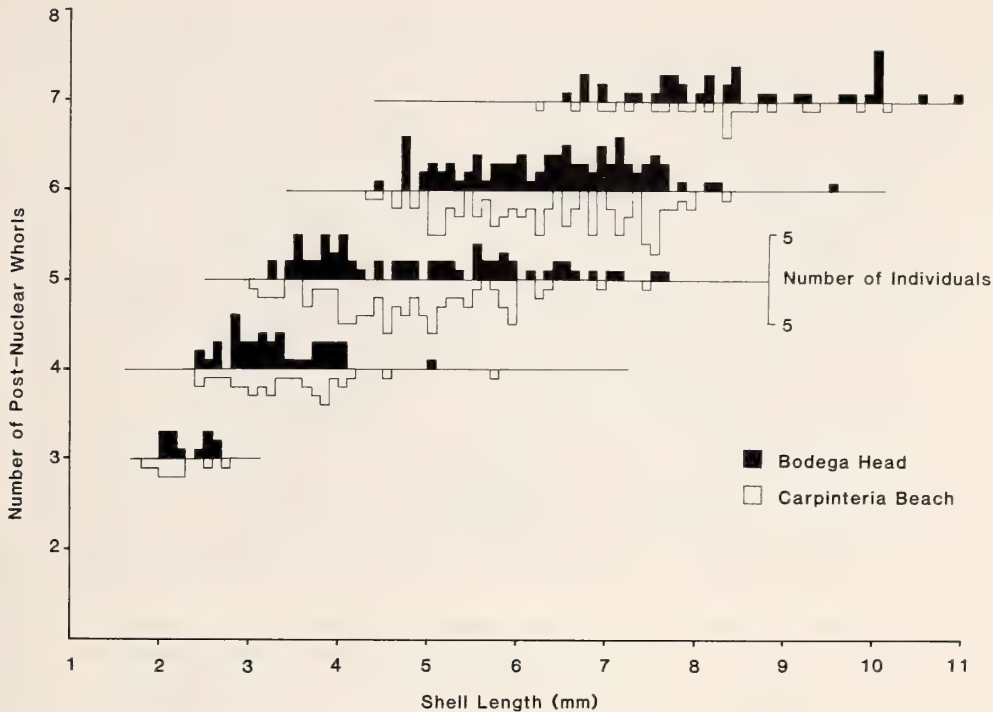


Figure 7

Comparison of *E. tinctorum* shell length and number of post-nuclear whorls. Along each line the numbers of individuals are arranged by collecting locality.

higher tolerances to desiccation, wave shock, and osmotic stress. Thus, a larger snail may be equipped to survive the harsher environment of higher latitudes better than a smaller snail.

Recently Breyer (personal observation) observed that southern California *Epitonium tinctorum*, collected from Santa Barbara and raised in the laboratory at the University of California, Santa Barbara, are capable of growing as large as northern California snails. At present we do not know why snails in the field in southern California do not grow as large as those collected in northern California.

Latitudinal variations in populations of *Epitonium tinctorum* closely resemble those found by FRANK (1975) for the black turban, *Tegula funebris* (A. Adams, 1855). In addition to finding larger snails in northern latitudes, Frank found that individuals in northern *Tegula* populations mature at a larger size and have irregular recruitment.

ROBERTSON (1981) reported similar size differences between populations of *Epitonium albidum* (Orbigny, 1842) in the British Virgin Islands and Barbados. The largest Virgin Island males were 8 mm long and females ranged to 16 mm. The largest Barbados Island males were 6 mm long while females reached 14 mm although most were 11 mm or less in length.

The northern California population of *Epitonium tinctorum* fluctuated in size and abundance more than the southern California population and had a definite periodicity. In winter, snail populations declined markedly in the north. Severe winters are known to cause increased mortality in intertidal molluscs unless animals can migrate or are passively washed to deeper waters, or unless they can escape into crevices to hide (CRISP, 1964). *Epitonium tinctorum* was difficult to locate among anemones during winter. It was assumed that most snails were washed off the rocks and died, but others may have escaped and lived out the winter in protected areas. Even if adults do survive the winter months, there is evidence that they may not increase in size appreciably until the spring. *Thais* (= *Nucella*) *lapillus* (Linné, 1758) grows little from October to March (LARGEN, 1967), and shell growth in *Tegula funebris* ceases completely from November to February (FRANK, 1975). The return of spring signifies a period of larval settlement and the cycle continues. Snails grow during summer and fall until the onset of winter storms. Southern California, in contrast to the north, generally has milder winters, calmer waters, and warmer temperatures. In the southern area it is common to see all stages in the life cycle of a snail throughout the year.

In the north, *Epitonium tinctorum* larvae may survive in

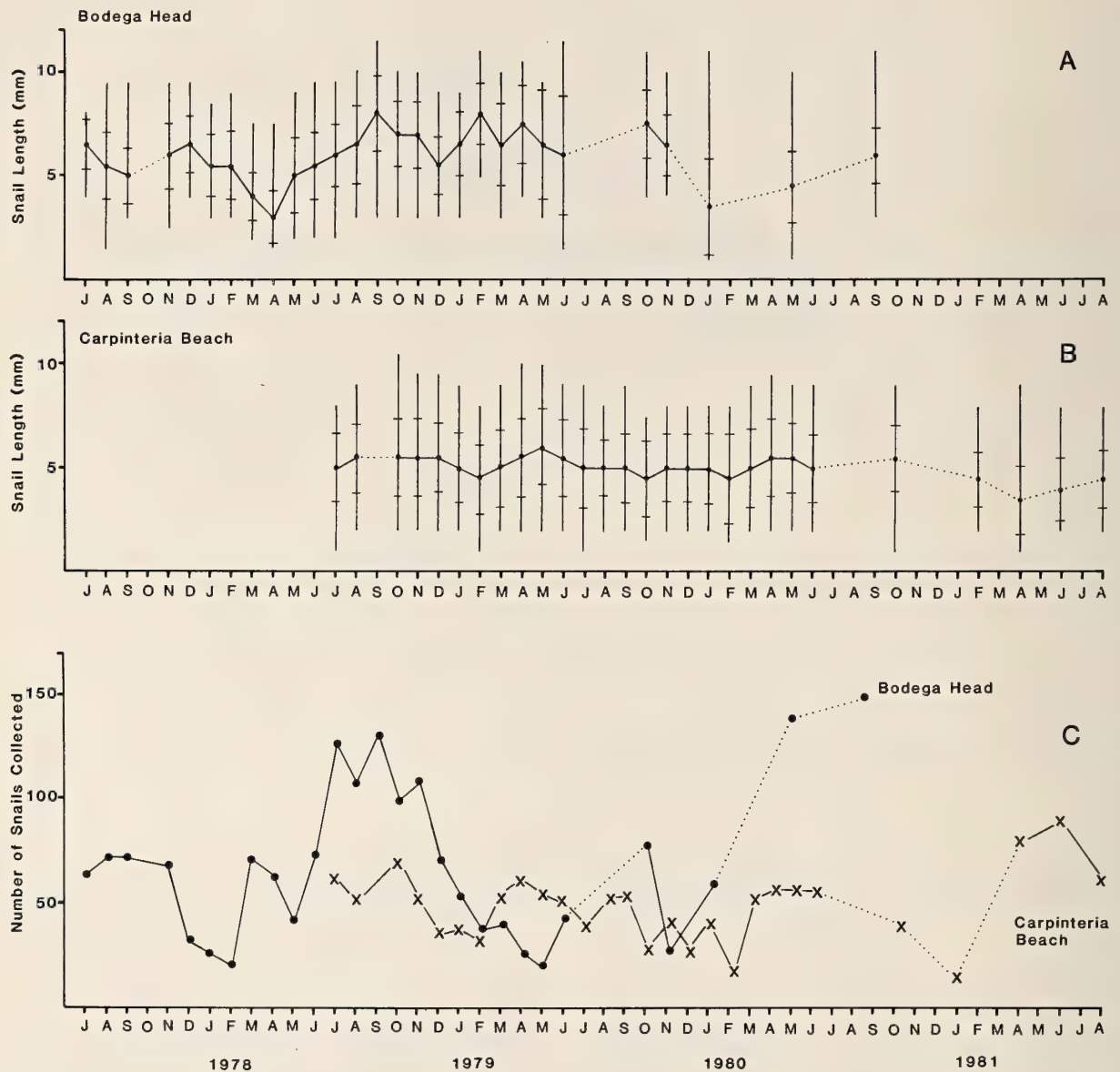


Figure 8

Size (including mean and standard deviation) and abundance of snails collected at Bodega Head and Carpinteria Beach from June, 1977, to July, 1981. A. Bodega Head, size. B. Carpinteria Beach, size. C. Bodega Head and Carpinteria Beach, abundance.

the plankton from late September until settlement, which often occurs as late as June. In the south, young snails and eggs are found throughout the year. Preliminary observations indicate the larvae of *E. tinctorum* grow considerably before they undergo metamorphosis. Before hatching, veligers of *E. tinctorum* measure about 70 μm in length. In the laboratory we have kept them alive for more than two months, at which time they had attained a size of more than 250 μm but had not yet metamorphosed. In the

field the smallest snail observed during more than two years of study was 1.1 mm; apparently, veligers grow considerably in the plankton before they settle. DEHNEL (1955) looked at growth rates of embryos and larvae of northern and southern gastropod populations. He concluded that the rates of growth of embryos and larvae in northern gastropod populations are often 2 to 9 times greater than in southern populations of the same species at a given temperature.

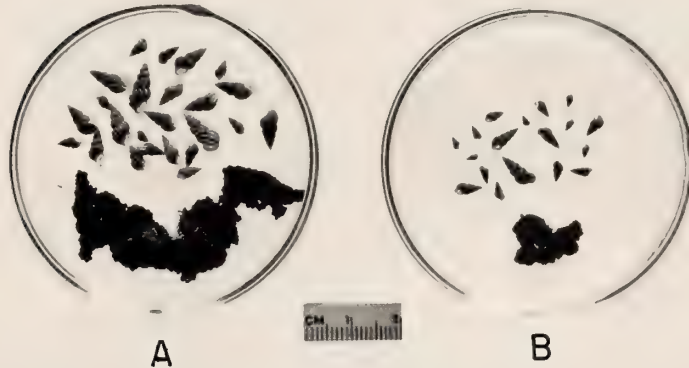


Figure 9

Comparison of the largest groups of snails and their associated egg masses found in fall 1980 collections. A. Bodega Head (26 September 1980; SBMNH 33878). B. Carpinteria Beach (23 October 1980; SBMNH 33879).

Once veligers metamorphose, growth in general is faster in warm than in cold seas, but this does not necessarily mean the largest species live in warm seas. The largest snails may be the slow-growing species found in cold water; and within a species, an individual is likely to grow more slowly, but become larger and older, at the northern limits of its distribution (FRANK, 1969). This theory is consistent with our observations. Larger *Epitonium tinctum* were found north of Bodega Bay in Fort Bragg, and the largest specimens were recorded from Forrester Island, Alaska, the northern limit of distribution for this species.

ACKNOWLEDGMENTS

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The Reproductive Cycle of the Trochid Gastropod *Oxystele variegata* (Anton, 1839)

by

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Abstract. *Oxystele variegata* (Anton, 1839) is a trochid gastropod found commonly in the southern African intertidal region. Monthly samples over a one-year period were examined for gonadal development by comparing dry somatic and gonadal tissue weights and histological sections. Mature oocytes and sperm could be found in monthly samples of the gonads of all animals over 10 mm in size throughout the year, but based on changes in gonadal weights two spawning peaks were detected—one in February and a second in September to October. It seems likely that this temperate species is able to spawn throughout the year but that spawning is intensified during these peak periods.

INTRODUCTION

Oxystele variegata (Anton, 1839) is a trochid gastropod which occurs commonly in the rocky intertidal zone in estuaries and along the southern African coast from southern Angola (KENSLEY & PENRITH, 1972) to Durban in South Africa (DAY, 1974). It is one of four species in the genus *Oxystele* that are found in the balanoid zone, where it is very prominent. Because of its abundance *O. variegata* must be a major contributor to the energy budget of this zone. Based on measurements of the metabolic rate of this species, KING (1974) estimated that the annual population production was $46.4 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. McQUAID (1980, 1982a) has described how the population of *O. variegata* is zoned according to size with the largest animals in the upper balanoid zone and the smallest lower on the shore. No attempt has yet been made to ascertain the breeding cycle with any certainty, but McQUAID (1980) hypothesized from settlement patterns that spawning occurred throughout the year, with a peak in February and two smaller peaks in May/June and September/October, 1977.

Monodonta lineata, a related trochid of the northern cool temperate regions, has been investigated by DESAI (1966), who found that this species spawned from May to August with male and female gonads showing similar cycles. UNDERWOOD (1972) investigated the breeding cycle of the British trochids *M. lineata*, *Gibbula umbilicalis*, and *G. cineraria*. He found that *M. lineata* and *G. umbilicalis* spawned throughout July and August and less in September. However, *G. cineraria* did not provide clear evidence

of spawning since histological sections of the gonads appeared the same throughout the year.

UNDERWOOD (1974) also found that the trochid *Austrocochlea constricta*, which occurs on the west and southwest coast of Australia, did not show any seasonal change in the appearance or histology of the gonad, and he concluded that this species spawned throughout the year with a peak in October/November. PAINE (1971), using energy content as a measure of reproductive state, concluded that the western North American trochid *Tegula funebris* spawned once a year during the summer.

In this paper a description is given of the breeding cycle of *Oxystele variegata*, based on changes in the ratio of gonadal/somatic dry weight and gonadal histology during the course of a full year.

MATERIAL AND METHODS

Monthly samples of *Oxystele variegata* were collected at random from the upper balanoid zone at Dalebrook on the Cape Peninsula (47°07'S, 18°27'E) during the period April, 1980, to March, 1981. The animals were preserved in a 5% formalin solution until they could be examined.

Fifteen to 20 animals of each sex were dissected each month. Every shell was measured across the base at the widest point and the animal was then removed and the operculum cut off and measured. The gonad was dissected out of the somatic tissue and both gonadal and somatic tissue were dried in an oven at 55°C for 24 h. The dry

Table 1

Mean monthly shell sizes and opercular diameters of *Oxystele variegata* sampled for gonadal development.

Month	Shell size (mm)		Opercular diameter (mm)	
	♂	♀	♂	♀
April, 1980	14.9	14.8	5.4	5.5
May	16.4	16.0	6.0	5.8
June	16.0	16.0	5.8	5.6
August	15.5	16.2	5.4	5.3
September	16.8	16.7	6.0	6.0
October	16.6	16.5	6.0	5.9
November	16.8	16.4	5.8	5.8
December	15.6	16.0	6.1	5.9
January, 1981	15.6	15.5	5.6	5.8
February	16.5	16.5	5.9	5.9
March	15.3	16.5	5.4	6.0
Annual mean	16.0	16.1	5.8	5.8

weights of the gonad and of the somatic tissue for each animal were measured.

In addition to the above animals, two to five specimens of each sex were collected each month and used to obtain histological sections of the gonads. The gonads of these preserved specimens were dehydrated in alcohol and blocked in paraffin wax. Transverse sections were cut through the center of the gonads at 10 μ m. The sections were dehydrated in alcohol and stained with hematoxylin and eosin.

The male and female gonadal weights were linearly regressed on somatic tissue weights for each month. The data obtained from these regressions were used to calculate monthly gonadal indices. These indices were defined as the ratio of gonadal to somatic weight, expressed as a percentage for a standard animal of 0.07 g somatic weight (with an opercular diameter averaging 5.8 mm).

RESULTS

All specimens dissected, ranging from 13.6 mm to 21.6 mm shell width, had mature gonads throughout the sampling period. Individuals of *Oxystele variegata* less than 10.0 mm shell width lacked gonads and progressively larger gonads could be found in animals with a shell width of 10.0 mm and upwards.

In both males and females of *O. variegata* the gonads lie adjacent to and above the digestive gland, extending into the shell spiral up to the apex. As with most archaeogastropods, trochids release the unfertilized gametes directly to the surrounding environment where fertilization occurs (FRETTER & GRAHAM, 1962; DESAI, 1966; PAINE, 1971; UNDERWOOD, 1972; BRANCH, 1974). *Oxystele variegata* probably conforms to this pattern since we observed no egg laying or egg masses. The male gonad is a pinkish, densely constituted tissue. Histological sections showed that

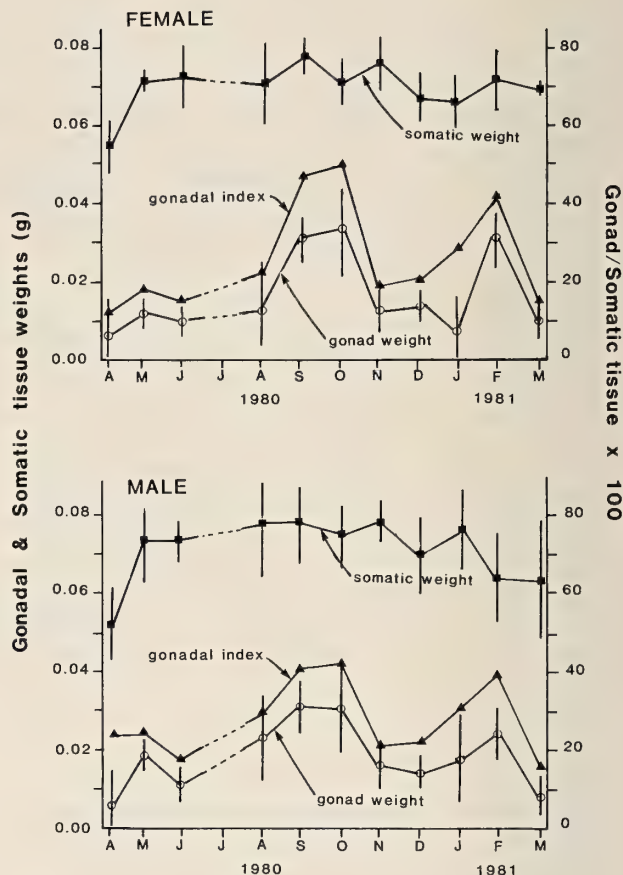


Figure 1

Gonadal and somatic dry tissue weights (g) of "standard" *Oxystele variegata* with an opercular diameter of 5.8 mm and the gonadal index (expressed as a ratio of gonad:somatic weight \times 100) plotted against time (month). (Bars indicate 95% confidence levels.)

there were ripe spermatozoa present throughout the year. The ratio of spermatozoa to spermatids and spermatocytes differed from individual to individual in the same month, but spermatozoa never constituted less than 50% of the area of the testis (as determined from grid counts of the gonadal sections). The female gonad contains a mass of white or creamy oocytes, each within a clear jelly coat which is a feature of the trochids (FRETTER & GRAHAM, 1962; DESAI, 1966; DUCH, 1969; UNDERWOOD, 1972, 1974; SIMPSON, 1977; WEBBER, 1977; HESLINGA, 1981). Mature oocytes were present throughout the year and had an average diameter of 180 μ m, not including the jelly coat. Histological sections showed immature oocytes were also present throughout the year, but not common from January to February or from August to September. No difference existed in mean shell or opercular diameters between the sexes of the animals sampled (Table 1).

The gonadal indices show strong correlation between the sexes, both peaking from September to October, 1980,

and in February, 1981, and both dropping in November, 1980, and March, 1981 (Figure 1). Since this gonadal index can be affected by changes in somatic weight, an independent assessment of changes in somatic and gonadal weights was also undertaken. Both gonadal and somatic weights were linearly regressed on opercular diameter for each month. These regressions are shown in Table 2. From these regressions the gonadal and somatic weights of animals with a standard opercular diameter of 5.8 mm could be calculated for each month. The somatic weights fluctuated about a mean of 0.07 g for each sex. As shown in Figure 1 the somatic weights of both sexes peaked above the mean in September and November and dropped below the mean in April. The gonadal weights of both sexes reflected the gonadal indices almost completely, thus confirming that in spite of slight changes in the somatic weight the gonadal index is a reliable measure of reproductive activity.

The number of non-significant correlations between gonadal weight and opercular diameter seen in Table 2 indicates a wide "scatter" amongst the population in certain months, particularly the males. This scatter is due to the fact that some individuals are sexually mature at a time when others have just spawned. Again, however, there was a strong correlation between the sexes for both the gonadal and somatic tissue weights, and we are confident that the gonadal index and changes of gonadal weights do reflect reproductive cycles.

DISCUSSION

It appears that *Oxystele variegata*, as with some other trochids (UNDERWOOD, 1972, 1974; SIMPSON, 1977) exhibits continuous gametogenesis once mature. Synchronization of spawning still remains important since fertilization is external and, indeed, the male and female gonadal weights do peak and fall in unison (Figure 1). *Oxystele variegata* congregates in large numbers in the upper balanoid zone at Dalebrook thus also ensuring proximity of the sexes during spawning. DESAI (1966), DUCH (1969), and SIMPSON (1977) also found this clustering behavior in trochids.

Despite this, the gonadal tissue weights (relative to opercular diameter) showed marked variation between individuals, particularly around the periods of peak spawning. However, in all samples dissected during other months there were always some specimens whose gonadal weights were well above or below the average and these were considered to be in pre- or postspawn states respectively. Such variation in the gonadal weights within the population probably indicates that there are some individuals that spawn out of phase with the bulk of the population. The presence of some spawned individuals in virtually every month of the year suggests that spawning occurs year round although peaking twice a year. These variations in gonadal weight are reflected in the number of months in which there were non-significant correlations

between gonadal weights and opercular diameter (Table 2), in contrast to the generally high correlations between somatic tissue weight and opercular diameter. The two main gonadal peaks indicate spring and late summer spawnings with the build up to the spring spawning (September to October) being more prolonged. At present we have no evidence whether these peaks repeat each year.

It is also apparent from the histological sections, which showed a constant supply of ripe ova and sperm in the gonads, and from the irregular but continuous settlement of recruits to the low shore (MCQUAID, 1982b), that spawning probably occurs throughout the year, peaking in the spring and late summer.

The somatic tissue weights of standard-sized animals of both sexes remained steady at a mean of 0.07 g, except for April when they declined. This fall in somatic weight is possibly because during this period there is a recruitment of new individuals to this zone (MCQUAID, 1982b) and we speculate that increased feeding competition may strain existing food sources. By May to June the population has declined due to mortality and the somatic weight increases (Figure 1) together with new algal growth in autumn. In the upper balanoid zone, from where our samples were taken, there are only two main macroalgae—*Porphyra capensis* and *Gelidium pristoides*. MCQUAID (1980) found that both these species have varied calorific values during the year. *Porphyra capensis* declined in calorific value during autumn whilst *G. pristoides* had a maximum value in autumn. The drop in calorific value of some of the food available for *Oxystele variegata* could affect the somatic weights, but we found that *O. variegata* were not commonly seen on macroalgae, and they possibly mainly feed on microalgae and sporelings rasped from the substratum. This is also the opinion of MCQUAID (1982a). A drop in the number of sporelings has been found during April in an analysis of monthly colonization carried out by Joska (in preparation) and this, too, could explain the lower somatic weight during this month.

In archaeogastropods the larval stage is brief (FRETTER & GRAHAM, 1962; DESAI, 1966; UNDERWOOD, 1972; WEBBER, 1977) and settlement on the shore should take place within a week of spawning. MCQUAID (1982a, b) found that 5 to 6-mm specimens of *O. variegata* were detectable in large numbers in February with a smaller peak in June/July. In addition, small numbers could be found throughout the year. Since specimens of *O. variegata* take about four months to reach a size of 5 to 6 mm, these juveniles probably settled about four months earlier, and are likely to have been the result of, respectively, the spring and late summer spawnings that we have recorded.

Temperature is a factor often cited as being of great importance for spawning or reproduction in marine invertebrates. During the period of sampling the sea temperatures rose during the spring spawning but fell at the time of the late summer spawning (Figure 2). Apart from suggesting that a minimum temperature exists for spawning, there is no obvious influence of temperature on the

Table 2

Regression coefficients for regressions of gonad weight (y) on operculum diameter (x): $y = a_0 + a_1x$ and coefficients of determination (r^2) with the probability that r^2 is significant (P).

	Month	a_0	a_1	r^2	P
♀	April, 1980	-0.0155	0.0382	0.2729	0.05
	May	-0.0340	0.0794	0.4638	0.001
	June	-0.0152	0.0436	0.2915	0.05
	August	0.0194	-0.0046	0.0026	Not significant
	September	-0.0290	0.1103	0.2988	0.01
	October	-0.0034	0.0630	0.0232	Not significant
	November	-0.0252	0.0672	0.3400	0.01
	December	-0.0093	0.0399	0.2495	0.05
	January, 1981	0.0058	0.0251	0.0214	Not significant
	February	-0.0676	0.1691	0.5365	0.001
	March	-0.0281	0.0666	0.5426	0.001
♂	April, 1980	-0.0222	0.0531	0.1509	Not significant
	May	0.0374	-0.0317	0.0228	Not significant
	June	-0.0661	0.1363	0.5817	0.001
	August	-0.0017	0.0439	0.1618	Not significant
	September	-0.0310	0.1093	0.1910	0.05
	October	-0.0195	0.0870	0.1710	0.05
	November	-0.0152	0.0535	0.4046	0.01
	December	0.0020	0.0231	0.1047	Not significant
	January, 1981	-0.0239	0.0707	0.1925	0.05
	February	-0.0820	0.1823	0.6314	0.01
	March	-0.0156	0.0433	0.0940	Not significant

Regression coefficients for regressions of somatic tissue weight (y) on operculum diameter (x): $y = a_0 + a_1x$ and coefficients of determination (r^2) with the probability that r^2 is significant (P).

	Month	a_0	a_1	r^2	P
♀	April, 1980	0.0346	0.0317	0.9934	0.001
	May	-0.1638	0.4054	0.8411	0.001
	June	-0.0601	0.2269	0.4540	0.01
	August	0.0622	0.0144	0.0049	Not significant
	September	-0.0863	0.2825	0.7607	0.001
	October	-0.1844	0.4410	0.7384	0.001
	November	-0.0926	0.2923	0.5173	0.001
	December	-0.0940	0.2788	0.4958	0.001
	January, 1981	-0.1105	0.3049	0.7235	0.001
	February	-0.1199	0.3335	0.5736	0.001
	March	-0.1688	0.4166	0.8663	0.001
♂	April, 1980	-0.0229	0.1282	0.4085	0.01
	May	-0.0199	0.1610	0.2331	0.05
	June	-0.1480	0.3823	0.5455	0.001
	August	0.0370	0.0659	0.1417	Not significant
	September	-0.1046	0.3129	0.6867	0.001
	October	-0.1327	0.3571	0.8634	0.001
	November	-0.0941	0.2979	0.6955	0.001
	December	-0.0296	0.1709	0.5703	0.001
	January, 1981	-0.0758	0.2295	0.6760	0.001
	February	-0.1319	0.3389	0.8117	0.001
	March	-0.1237	0.3222	0.5280	0.001

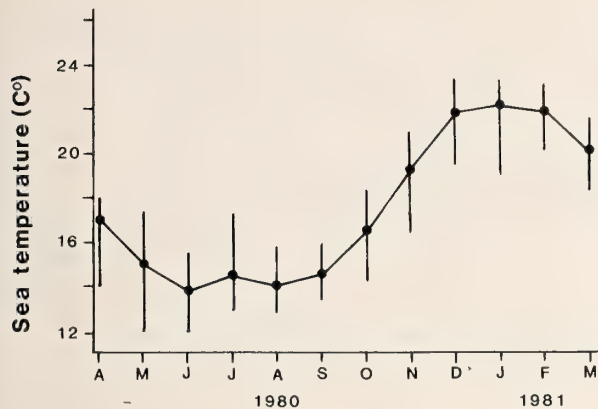


Figure 2

Mean monthly sea temperatures during the sampling period. Bars indicate maximum and minimum temperatures. (Temperature records kindly supplied by the Department of Maritime Defence, Simonstown.)

reproductive cycle in this species. Dalebrook lies in False Bay, which because of its shallow waters and current patterns affords year round moderate conditions and predictable seasonal changes in temperature. Rather more variant conditions on the west coast could possibly produce different spawning peaks.

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The Larval Biology of *Brachidontes modiolus* (Linné, 1767) (Bivalvia: Mytilidae)

by

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Abstract. Larvae of *Brachidontes modiolus* were reared in the laboratory from eggs through to settled juveniles. Egg sizes ranged between 67.3 and 77 μm . Straight-hinge veligers appeared 15 to 17 h after fertilization of the eggs. The length of shelled larvae increased from 96 to 221 μm : the straight-hinge stage from 96 to 176 μm , the umbo stage from 168 to 221 μm , and the pediveliger stage from 180 to 221 μm . Settlement occurred at lengths of 180 μm and upwards. The larval hinge consists of small teeth along the length of the hinge with larger teeth at both ends. Larvae of *B. modiolus* develop more rapidly and settle at an earlier age than larvae of *B. recurvus* and *B. granulata*.

INTRODUCTION

Brachidontes modiolus (Linné, 1767) (= *B. citrinus*) is a small marine mytilid, the adults of which measure between 38 mm (ABBOTT, 1974) and 46 mm (MCLEAN, 1951). The geographic range for this species is from Florida to the West Indies (ABBOTT, 1974). In Barbados, members of this sublittoral species may be found recessed within beds of the seagrass *Thalassia testudinum* König or attached to the rocky surface of reef flats at depths of 0–2 m. *Brachidontes modiolus* is highly gregarious and, whether living epifaunally or infaunally, occurs in dense aggregates of individuals.

The specific name *Brachidontes citrinus* (Röding, 1798) has been widely used. ABBOTT (1974), however, considered this to be a synonym of *B. modiolus* (Linné, 1767). Indeed the name 'modiolus' is singularly apt, for *B. modiolus* exhibits characteristics of the *Modiolus* group of mytilids, namely the possession of subterminal umbones and a shell shape which is more conical than triangular (STANLEY, 1970, 1972).

The larval biology of *Brachidontes modiolus* has hitherto been unreported in the literature under any of its synonyms. A knowledge of the duration of the planktonic stage of an aquatic larva, the time during which it is exposed to ocean or coastal currents, could contribute to an understanding of the distribution of a species in a given region. This aspect has been discussed by COE (1953) and SCHELTEMA (1971). In addition, a description of the larval stages of *B. modiolus* would aid in the identification of these larvae when encountered in plankton samples, as

well as establish the life history pattern and strategy of the species.

The identification of bivalve larvae has posed problems in the past. LOOSANOFF *et al.* (1966) drew attention to the inadequacy of "indirect methods" of identification of bivalve larvae, and pointed out that these methods have led to discrepancies in the description of larvae of the same species when reported by different authors. Indirect methods include monitoring the development of an unidentified larva found in the plankton through to settling and the assumption of identifiable features of a particular species. These authors recommend "direct methods" of identification, *i.e.*, the rearing of larvae from fertilized egg stage through to metamorphosis under controlled laboratory conditions. The development of reliable methods for obtaining viable gametes and for the rearing of juveniles has resulted in the successful culture of the larvae of several marine bivalves. LOOSANOFF & DAVIS (1963) reviewed methods for the cultivation of larvae and detailed the specific requirements necessary for the successful culture of 19 species of bivalves. As characters to be used in the identification of marine bivalve larvae, LOOSANOFF *et al.* (1966) listed the dimensions of the larval shell (the prodissoconch), its general shape, prominence of the umbones during growth to metamorphosis, and ratios of length of hinge to maximum length or width of shell. CHANLEY & ANDREWS (1971) and CHANLEY & CHANLEY (1980) provided useful terminology for describing larval shell form and, in order to provide a better description of larval shell length, height and depth relationships. LOOSANOFF *et al.* (1966) provided a guide to the dimensions and shapes of

20 species of bivalves, and CHANLEY (1970) gave a review of the larval characteristics of the Mytilidae. Within the genus *Brachidontes*, descriptions of the larvae of *B. recurvus* from the western North Atlantic Ocean have been published in CHANLEY (1970), and of *B. granulata* from central Chile in CAMPOS & RAMORINO (1980). The larvae of *B. senhousi* were described in YOSHIDA (1937), but according to KURODA *et al.* (1971; cited in CAMPOS & RAMORINO, 1980), this species belongs to the genus *Musculus*.

The purpose of this paper is to provide a description of the larval stages of *Brachidontes modiolus*, with information on the development and length of the larval life of the species.

MATERIALS AND METHODS

Gametes were obtained from ripe mussels collected during the peak of the reproductive season (June to September). This peak was determined by continuous sampling and histological techniques over a period of two years. In the laboratory the animals were cleaned of sediment and encrustations and placed in freshly collected sea water. Initially, several methods were employed in an attempt to obtain viable gametes:

- (1) temperature shock within the range 24–34°C;
- (2) pricking of the posterior adductor muscles of the adults;
- (3) introduction of sperm and/or eggs obtained from stripped gonads to water containing ripe mussels;
- (4) treatment of stripped gonads with a 0.1 N solution of ammonium hydroxide;
- (5) exposing the mussels to hydrogen peroxide in alkaline (pH 9.1) sea water as per MORSE *et al.* (1977). Only this last method was successful; hence, the procedure is detailed below.

Alkaline sea water was prepared with predetermined quantities of Trizma*, hydrochloric acid and natural sea water (pH 7.2). Three or four mussels were placed individually or collectively in beakers containing 50 ml of alkaline sea water per animal (pH 9.1); hydrogen peroxide was then added with a micropipette to a final concentration of 5 mM. This was the treatment solution. The animals were kept in this solution for one hour, after which time the liquid was decanted and replaced with 100 ml of fresh treatment solution. One hour after the second treatment, the mussels were removed from the alkaline sea water, rinsed, and placed in beakers containing 100 ml of natural sea water. These were then placed in a water bath at a temperature of 33–34°C. Males and females received the same treatment. The onset time of spawning varied widely, from 30 minutes to several hours after treatment in the hydrogen peroxide solution. Mus-

sels seen spawning were removed and placed individually in beakers containing natural sea water at 28°C. The eggs were rinsed thoroughly with sea water filtered through glass fiber filter paper. Sperm was added to the egg suspension, and the two allowed to remain undisturbed for 10 min to encourage fertilization. In some instances a female in the process of spawning was placed in a weak sperm suspension, and so the eggs were fertilized as they were extruded. The fertilized eggs were rinsed to remove excess sperm and placed in 150 ml of filtered sea water in Erlenmeyer flasks of 250 ml capacity. Possible contamination of the cultures was reduced by placing tissue paper in the necks of the flasks and covering the opening of the flask with aluminum foil. If flasks containing larvae were left open to the air, a dense population of ciliates soon developed, with consequent death of the larvae. The embryos were left undisturbed for 24 h, at which time the strongly swimming larvae were pipetted off and introduced into fresh sea water to a density of 25–30 larvae/ml. The water containing the larvae thereafter was changed every third day. This was achieved by washing the larvae over a fine nylon mesh which was glued securely over one end of a large open-ended glass tube. Mortality of the larvae during washing was reduced if the mesh was held in a beaker containing filtered sea water, so that the mesh was positioned below the surface of the water. The bottom layer of water in the flask was discarded as dead or weak larvae accumulated there. The flasks were thoroughly washed at each water change, and care was taken to ensure that no detergents contaminated the sea water. The sea water used for each change was freshly collected and filtered. Best survival rates were obtained when the larvae were reared in unaerated sea water.

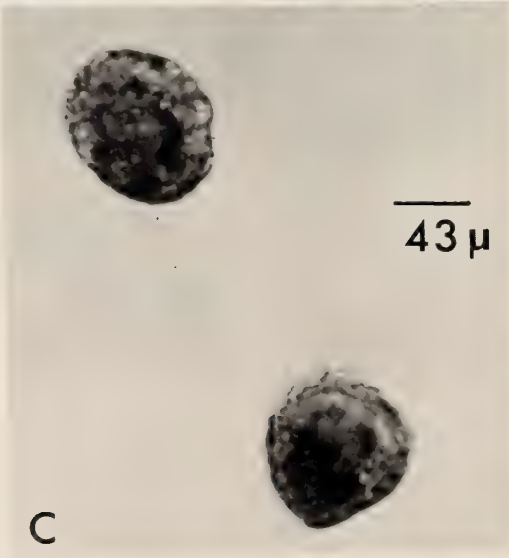
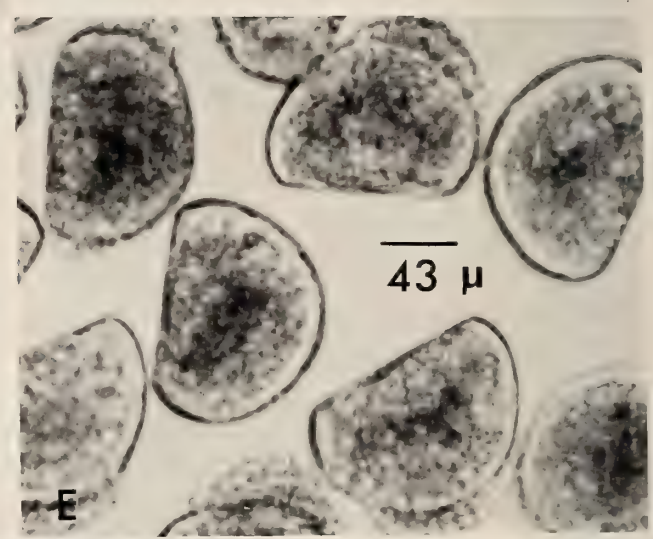
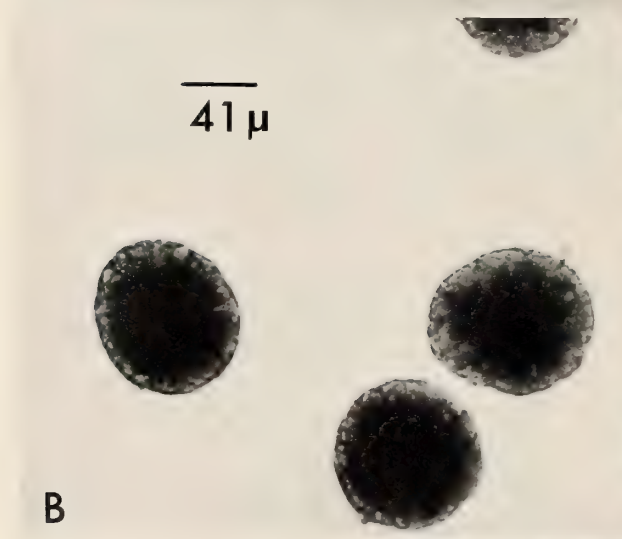
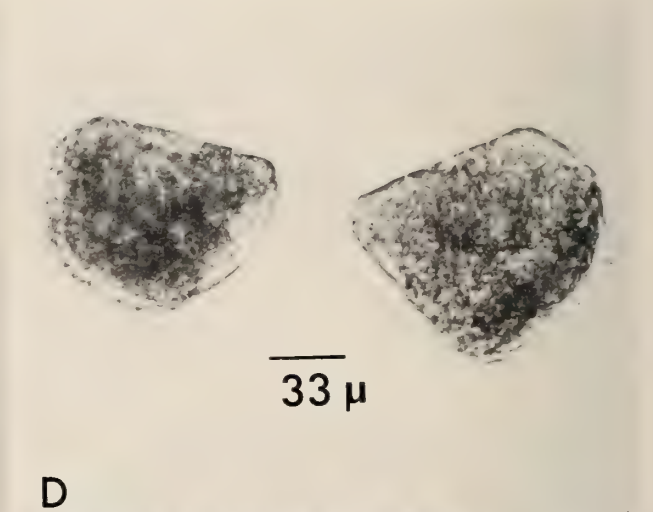
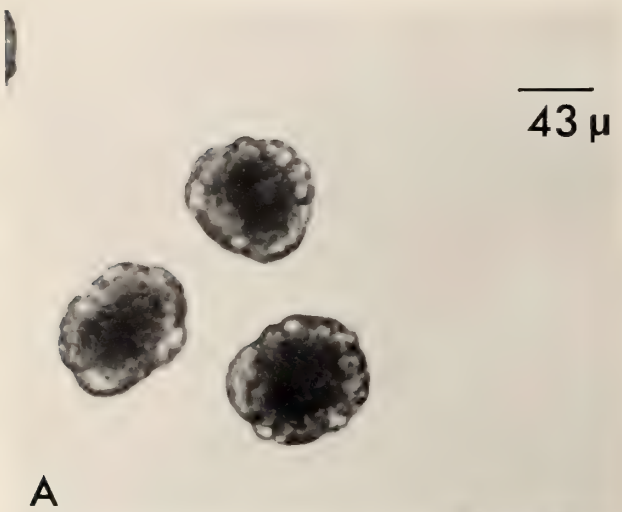
The larvae remained unfed for 48 h and thereafter were fed on a mixture of *Dunaliella tertiolecta* and *Nephroselmis tibron*. When possible, *Isochrysis galbana* was added to the diet. Feeding densities in the case of the larger alga, *i.e.*, *Dunaliella*, was approximately 8000–10,000 cells per ml of culture solution. Concentrations of the smaller alga were higher, 70,000–80,000 per ml of culture solution. Algal concentrations of these magnitudes were cleared by the larvae in 24 h.

Sub-samples of approximately 10 larvae were measured every two days for two weeks. Length was measured as the maximum distance in the antero-posterior direction, height as the maximum distance from the hinge to the ventral margin of the shell, and depth as the maximum left-right dimension (CHANLEY, 1970).

RESULTS

The eggs of *Brachidontes modiolus* ranged in diameter from 67.3–77 μm , and were a uniform dark brown in color. When spawned, the eggs had an irregular appearance but soon became rounded. No measurements were made of the spermatozoa. The sperm obtained from stripped go-

* A brand name. Use here does not necessarily imply endorsement of the product.



nads appeared less active than those obtained through the mediation of hydrogen peroxide.

As in BAYNE (1965), the stages chosen to evaluate development times to the straight-hinge stage were those easily recognized and not those with particular embryological significance (Table 1).

Stage 1—First division: the time at which 50% of the sample had undergone first cleavage.

Stage 2—The ciliated blastula: first appearance of cilia, evidenced by slowly rotating larvae (Figure 1a).

Stage 3—The early trochophore: appearance of an apical flagellum (Figure 1b).

Stage 4—Veliger: appearance of long cilia on the apical plate (Figure 1c).

Stage 5—Transitional stage: first appearance of the shell as a transparent object on the dorsal surface of the larva (Figure 1d).

Stage 6—Straight-hinge veliger: the possession of a complete shell, the prodissococonch. Very early straight-hinge veligers are darker than the later ones (Figure 1e).

First division occurred approximately 36 min after fertilization and the ciliated blastula appeared 3 h later. The ciliated blastulae swam slowly at first and as time progressed swam upwards towards the surface of the water column. Development of the trochophore occurred 5 h after fertilization, and veligers were first seen 4 h later. Transitional stages between the veliger and the straight-hinge veliger appeared 12 h from zero time, and straight-hinge veligers were seen in cultures 15–17 h after fertilization. The color of the larvae underwent a change during development, and stages 1 through 5 were dark brown while stage 6, the straight-hinge veliger, was a pale yellow-brown.

The rate of development of the larvae varied with temperature. Larvae reared at 34°C developed into straight-hinge veligers 13 h after fertilization. In cultures kept at 24°C, it was not until 25 h had elapsed that straight-hinge veligers were observed. At the time that straight-hinge veligers were recorded from cultures reared at 28°, 32° and 34°C (*i.e.*, between 13–17 h), larvae reared at 24°C were still at the early trochophore stage.

Larval Dimensions and Shape

The early straight-hinge larvae measure 96 μm in length, with a minimum height of 67 μm . No measurement of depth was recorded at the earliest straight-hinge stage. The smallest depth recorded was 56 μm at a larval length

Table 1

Summary of the observed development times of the larvae of *Brachidontes modiolus*. Temperature = 28°C.

Stage	Description	Time
0	Fertilization	0
1	First division	34–36 min
2	Ciliated blastula	3 h 40 min
3	Early trochophore	5 h 15 min
4	Veliger	9 h 15 min
5	Transitional stage	12 h
6	Straight-hinge veliger	15–17 h

of 152 μm . Straight-hinge larvae attained a size of up to 176 μm in 6 days. Heights then ranged from 126–144 μm , and depths from 84–104 μm . At lengths greater than 176 μm the hinge line invariably showed signs of rounding (Figure 2). Lengths increased faster than height, which in turn increased faster than depth. Between lengths of 96 and 115 μm , heights were 19–29 μm less than length, while at a length of 176 μm , heights measured 32–50 μm less than length. The first indication of umbo development appeared at 168 μm , with heights ranging from 120–136 μm and depths from 72–88 μm . All observed combinations of larval heights and depths for a given length are given in Figure 3. The length of the hinge at a shell length of 152 μm was 120 μm , increasing to 128 μm at a shell length of 168 μm . The results are summarized in Table 2 and Figure 2.

The straight-hinge larva is roughly "D" shaped. The hinge line is long relative to the length of the shell. The shoulders slope steeply, with the posterior shoulder shorter and sloping more steeply than the anterior. The posterior end is higher and more pointed than the anterior. The ventral margin of the shell is rounded. The hinge line becomes slightly rounded with the development of the umbo, and is at first "round" or "indistinct." The umbo may remain low and not clearly defined through lengths of 168–288 μm , becoming "broadly rounded" in later stages. The minimum length at which the umbo was seen to project above the shell margin is 240 μm . The shoulders at this stage are almost straight, the anterior shoulder not sloping as steeply as the posterior. The ventral margin is now markedly elongate, but still rounded. The larval hinge consists of a series of small teeth, flanked by two or three larger teeth.

Figure 1

Stages in the early larval development of *Brachidontes modiolus*. A. ciliated blastula; B. early trochophore; C. veliger; D. transitional stage; E. straight-hinge stage.

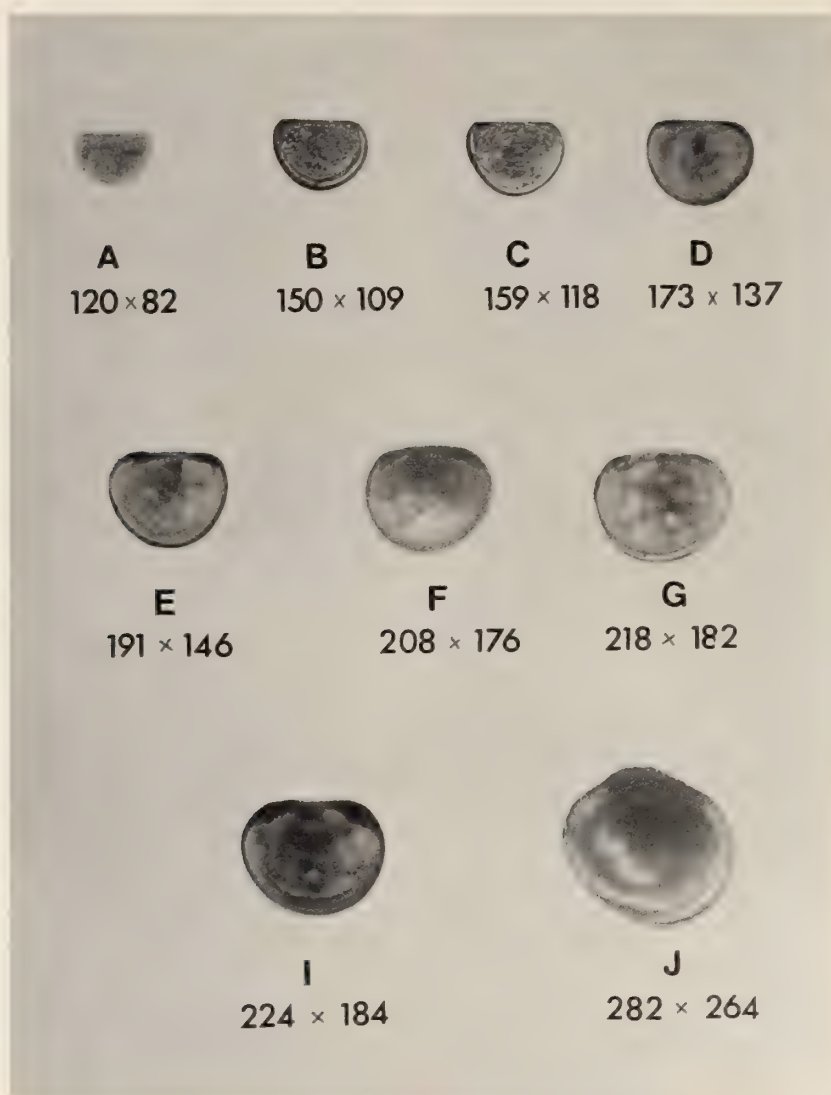


Figure 2

The larvae of *Brachidontes modiolus* at different stages of development from the early straight-hinge stage (A) to settlement (G-I). Larvae are positioned with anterior end to the left, except in J. The larva in J is an early juvenile just beginning dissoconch growth. The length and height of the larvae are indicated under each photograph; measurements are in microns.

The smallest pediveliger larva seen using its foot measured 180 μm (Figure 4) in length, but more generally, ambulatory pediveligers appeared at a length of 184 μm . The eye spot first appeared in larvae at length 184 μm when cultured at temperatures of 32° and 34°C.

Internal Anatomy of the Larvae

The internal anatomy of the larva was at first indistinct at magnifications of up to 500X. The gut became apparent on the first day as a straight tube running in a posterior

direction. It soon became coiled (Figure 5a). The digestive gland soon became easily visible, as with the onset of feeding in the larvae, the organ developed a green-brown color (Figure 5b). The adductor muscles showed clearly by the third day, and the velar retractor muscles were also conspicuous at this time. The foot was fully developed by day 6, with the pedal retractor muscles clearly visible (Figure 5c, d). The velum increased in size with the development of the larva to the pediveliger stage, and occupied a large portion of the shell cavity. The gill filaments were not clearly visible until after metamorphosis (Figure 5e). The

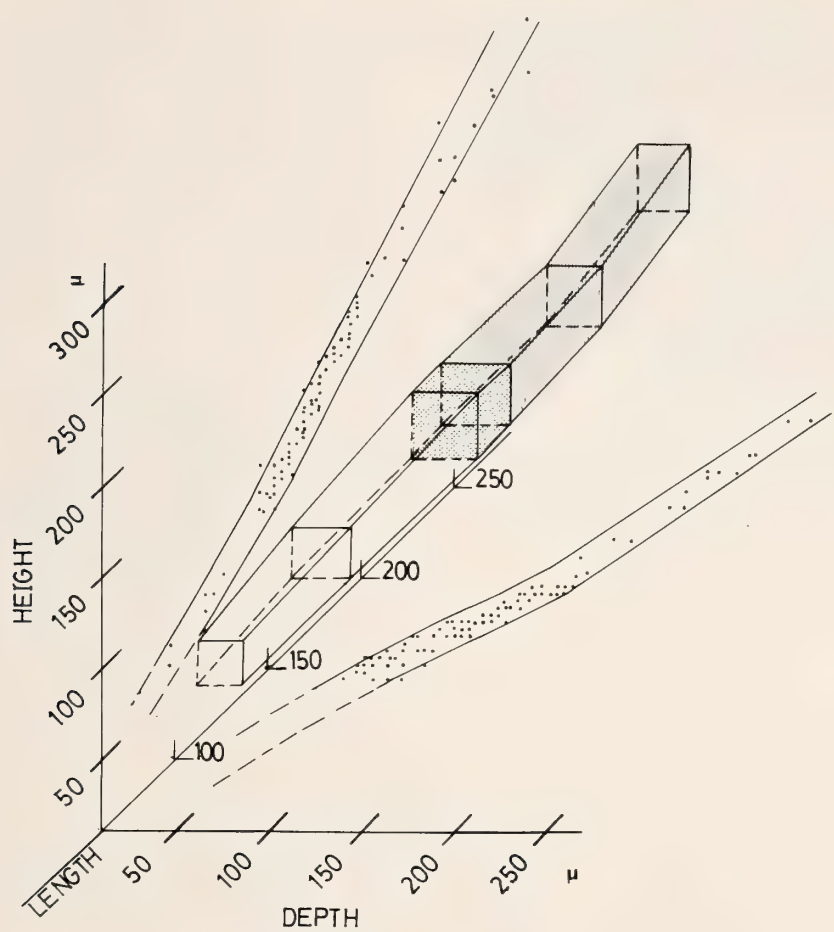


Figure 3

Larval dimensions of *Brachidontes modiolus*. The height and depth co-ordinates run parallel to the length axis. The dots represent length-depth or length-height measurements. The lines enclosing the dots were fitted by eye and represent maximum and minimum height and depth measurements. The three-dimensional figure represents all possible length, height, and depth combinations for *B. modiolus* (after CHANLEY & VAN ENGEL, 1969). The clear area represents the straight-hinge stage, the lined area the umbo stages, and the stippled area, the transitional stage between straight-hinge and umbo forms.

larvae of *Brachidontes modiolus* settled at sizes between 180 and 221 μm in length and settlement occurred from day 11 onward, although swimming larvae were still visible in the medium up to the 30th day.

DISCUSSION

Induction of Spawning

LOOSANOFF & DAVIS (1963) list methods used in the induction of spawning in 19 bivalves. They pointed out that where some species responded to thermofluctuation as a stimulus to spawning, others needed the additional stimulus of a sperm or egg suspension. In some instances special methods had to be employed, such as pricking the

Table 2

Summary of larval dimensions of *Brachidontes modiolus*.

Stage	Length (μm)	Height (μm)	Depth (μm)
Early straight-hinge stage	96	76	*
Straight-hinge stage	96-176	67-152	*-100
First indication of umbo	168	120-136	72-88
Umbo stage	168-221	120-184	72-124

* Not measured.

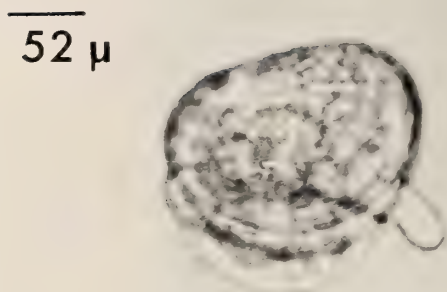


Figure 4

Pediveliger of *Brachidontes modiolus*.

adductor muscle in *Mytilus edulis*. Other species, like *Modiolus demissus*, did not respond to any treatment; LOOSANOFF & DAVIS (1963) were unsuccessful in inducing this species to spawn. WILSON & HODGKIN (1967) failed to induce spawning of *Brachidontes cf. variabilis* in the laboratory. CHANLEY (1970) was finally successful in causing spawning in *B. recurvus* by placing the mussels in sea water with temperatures fluctuating between 20 and 32°C. Previous attempts to induce spawning in this animal, by adding stripped gametes to the water or stretching or injuring the adductor muscles, had proved unsuccessful. Ripe adults of *B. granulata* spawned when placed in filtered sea water at 16°C after being held in an incubator at 6°C for 12 h. The account presented above demonstrates the individuality of the response of different species to various spawning stimuli.

Stripping of the gonad of *Brachidontes modiolus* failed to produce viable gametes for the same reason that the eggs obtained through the mediation of 0.5 M KCl are not fertilizable. RAVEN (1958) stated that maturation of the eggs of most mollusks may begin spontaneously, independent of fertilization, e.g., after spawning in sea water, and continues until metaphase of the first maturation division. Unfertilized eggs are blocked at this stage. Maturation is evidenced in part by the dissolution of the germinal vesicle. The ova of *B. modiolus* are not mature while still in the gonad. Eggs from this species, when obtained by stripping or by injection of KCl, possessed an intact germinal vesicle and were therefore immature and were incapable of being fertilized without further treatment (e.g., the addition of NH_4OH). In contrast, the eggs extruded from mussels stimulated by the addition of hydrogen per-

oxide had started the maturation process and were easily fertilizable.

MORSE *et al.* (1977) found that the hydrogen peroxide-induced spawning of the abalone *Haliotis rufescens* may have resulted from a "direct activation of the enzyme-catalyzed synthesis of prostaglandin endoperoxide." Prostaglandin endoperoxide (PGE₂) is produced from arachidonic acid through a series of reactions, the first step of which is catalyzed by the enzyme fatty acid cyclooxygenase (=PGE₂ synthetase). These investigators showed that abalone eggs and gonads from ripe animals of both sexes contained large quantities of cyclooxygenase, and further that hydrogen peroxide directly increased the rate of the reaction catalyzed by the PGE₂-forming cyclooxygenase from reproductive cells of the abalone. PGE₂ synthetase has been implicated in the control of spawning not only in abalones, but in *Mytilus californianus* (MORSE *et al.*, 1977) and sea urchins (MORSE *et al.*, 1978). It is probable that a similar control of spawning exists in *Brachidontes modiolus*. IWATA (1952) found that electrical stimulation induced maturation of eggs of *Mytilus edulis*. He suggested that the stimulus was mediated by the ovary, probably by the secretion of some substance that caused the ova to mature. According to IWATA (1952), spawning in *Mytilus* appeared to follow automatically as soon as the eggs begin the maturation division, and therefore spawning in this animal depended entirely on whether the maturation process had taken place. A number of questions arise from a comparison of the results of MORSE *et al.* (1977) and IWATA (1952). Could the proposed substance of IWATA (1952) be related to PGE₂ synthetase, or to any of the enzymes or intermediate products of PGE₂ production? Conversely, does PGE₂ synthetase act to promote maturation of oocytes and hence spawning?

The role of PGE₂ synthetase in the control of spawning in *Brachidontes modiolus* would be of interest for further study. MORSE *et al.* (1977) stated that the fatty acid-cyclooxygenase reaction may be potentially rate-limiting in the physiological sequence of reactions leading to spawning and therefore possibly under hormonal and/or neural control. Thus a knowledge of the levels of this enzyme in *B. modiolus*, together with information on environmental factors, could help in determining the ultimate factors controlling the release of gametes in this species.

Larval Survival and Development

Larvae survived well in unaerated cultures, and change of water every third day proved adequate for removing toxic waste products before harmful levels were reached. Some morphological malformations were observed in some of the larvae, for example concavity of the hinge line or unequal valve growth; but it could not be determined to what extent these were due to culture conditions. Abnormality of the hinge line as seen in *Brachidontes modiolus* was also reported for other bivalves (LOOSANOFF & DAVIS, 1963). In addition, these authors described another type

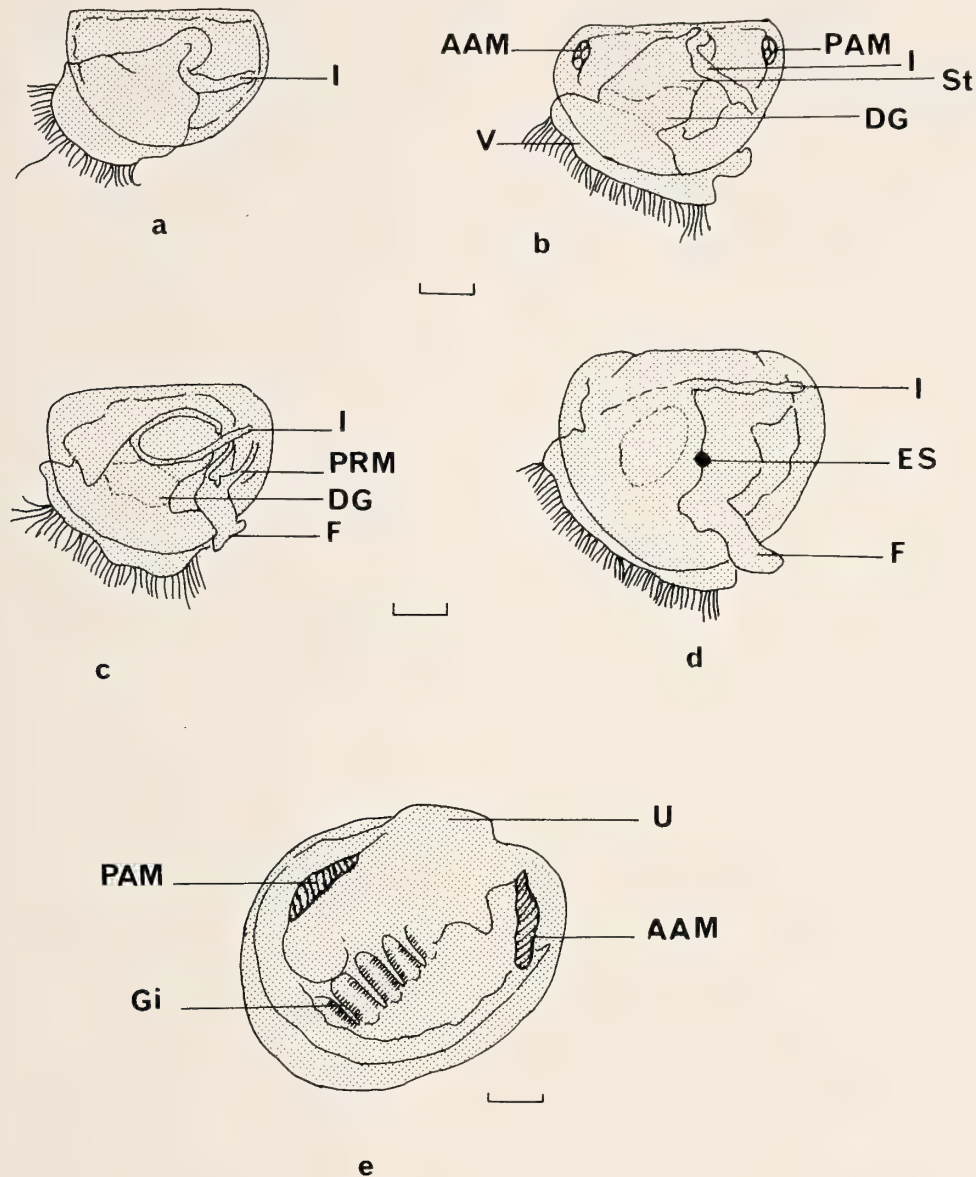


Figure 5

Diagrams of conspicuous features of the internal anatomy of *Brachidontes modiolus*. a. straight-hinge veliger; b. 3-day old larva; c and d. 6-day old larvae; e. spat. Scale bar for a, b, c, and d is 40 μm long; for e, it is 60 μm long. AAM, anterior adductor muscle; DG, digestive gland; ES, eye spot; F, foot; Gi, gills; I, intestine; PAM, posterior adductor muscle; PRM, pedal retractor muscle; St, stomach; U, umbo; V, velum.

of larval abnormality in which there was no clear-cut anatomical malformation, but rather the larvae were unable to feed. Such larvae developed to the straight-hinge stage but grew no further and eventually died. It is probable that the larvae found in the bottom layers of cultures of *B. modiolus* suffered from this type of "feeding" abnormality. LOOSANOFF & DAVIS (1963) reported that this type of abnormality in *Mercenaria mercenaria* was related

in some instances to the type of food fed to the larvae. This aspect was not investigated in *B. modiolus*.

That larvae of various species of bivalves show variation in growth rate among individuals reared from the same spawn under similar conditions is well established (LOOSANOFF & DAVIS, 1963). In addition to individual variation in growth rate, larvae of *Brachidontes modiolus* settle at different times after 11 days. LOOSANOFF & DAVIS

Table 3

Summary of the major features of the larvae of *Brachidontes modiolus*, *B. recurvus**, and *B. granulata***.

Stage or distinctive feature	Size (μm)		
	<i>B. modiolus</i>	<i>B. recurvus</i>	<i>B. granulata</i>
Unfertilized egg	67–77	62–68	63–73
Straight-hinge veliger	96–176	90–165	177†
Appearance of umbo	168	135	150
Conspicuous eye spot	184	180	—
Pediveliger (first appearance of functional foot)	180	165	200

* Data taken from CHANLEY (1970).

** Data taken from CAMPOS & RAMORINO (1980).

† Length of prodissoconch.

(1963) found that the number of days needed for larvae of the same cultures to reach settling stage was not sharply defined, even for a culture reared under standard well-controlled conditions. The observed extended settling period of *B. modiolus* may be explained by the probability that glass is not the most desirable substrate for settling, as well as it may be related to factors governing settling density. Larvae possessing a functional velum could be seen swimming in the water column long after others in the same flask had settled and attached themselves by byssal threads. BAYNE (1965) discussed the delay of metamorphosis in *Mytilus edulis* and showed that the larvae become capable of attachment and metamorphosis some time before they would attach to glass, and that the majority died without attachment. The delay of metamorphosis of laboratory reared larvae has been previously reported for other bivalves: CULLINEY (1971) for *Lithophaga bisulcata*, CAMPOS & RAMORINO (1980) for *Brachidontes granulata*. BAYNE (1965) established that the larvae of *Mytilus edulis* settled preferentially on filamentous algae (primary settlement). The larvae of *B. modiolus* did not settle on algae provided in the culture flasks. However, in another experiment not described here, a fine filament of artificial fiber of unknown origin precipitated mass gregarious settlement of larvae of *B. modiolus*. In the wild population no sign of attachment to algae by the larvae of *B. modiolus* was recorded in this study.

CHANLEY (1970) described the common characteristics of larval Mytilidae. The larvae of *Brachidontes modiolus* exhibited many of the features listed. The hinge line was long in relation to larval length and increased in size with growth of the larvae. The hinge possessed a mytilid dentition, having a series of small teeth along the length of the hinge, with larger teeth towards the end. The umbo was late in developing and remained indistinct. In fact, it was not until after settling that the umbo of *B. modiolus* became pronounced. However, the larvae of *B. modiolus* set at a smaller size (180–221 μm) than most mytilid

larvae (300 μm , in CHANLEY, 1970) as do larvae of other species of this genus (Table 3).

A comparison of the development of the larvae of *Brachidontes modiolus*, *B. recurvus*, and *B. granulata* (Table 3) reveals differences in size at first appearance of the umbo and in minimum sizes of the pediveligers. The shape of the straight-hinge veliger of *B. modiolus* more closely resembles that of *B. recurvus* than that of *B. granulata*. The shape of this larval stage of *B. granulata* is more rounded than that of the former two. If, however, a comparison is made of later stages, the position is reversed, with the larvae of *B. granulata* being more similar in shape to that of *B. modiolus* than *B. recurvus*. The most notable difference is in the developmental times of the three species. Pediveligers first appeared after 6 days and settlement of the larvae of *B. modiolus* occurred from the 11th day onwards, similar to the time of the first appearance of pediveligers of *B. recurvus*. CHANLEY (1970) does not report on the time of settlement of *B. recurvus*. The pediveligers of *B. granulata* do not appear until 55 days after fertilization, and CAMPOS & RAMORINO (1980) report no evidence of metamorphosis up to 33 days after this. This lack of metamorphosis in the larvae of *B. granulata* was attributed to the unavailability of a substrate suitable for settlement of the pediveligers. The variation in the developmental times may result from the different temperature regimes to which the larvae were exposed. The larvae of *B. granulata* were reared at 12–16°C, those of *B. recurvus* at 25°C, and the larvae of *B. modiolus* at 28°C. BAYNE (1976) presented data from various authors on the rates of cleavage and early development of *Mytilus edulis* at different temperatures (8–22°C). Those results showed that development proceeded more rapidly at the higher temperatures.

In general the developmental progress and morphology of the larvae of *B. modiolus* closely resemble those of the larvae of the other two members of the genus *Brachidontes* described in the literature. In the early stages the larvae of *B. modiolus* bear strongest resemblance to those of *B. recurvus* while at later stages the more obvious resemblance is to the larvae of *B. granulata*. These findings tend to reinforce the family or group relationships of these three species. The most outstanding difference is in the developmental times, with *B. modiolus* settling the earliest of the three.

This difference has been attributed to different temperature regimes at which the larvae were reared. *Brachidontes recurvus* was reared at 25°C, *B. granulata* at temperatures between 12° and 16°C; and *B. modiolus* at 28°C.

ACKNOWLEDGMENTS

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A Comparison of the Species Richness and Trophic Roles of Gastropods and Chitons on Rocky Shores of Temperate and Tropical West America

by

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Abstract. I examined local species richness and trophic roles of gastropods and chitons in rocky intertidal zones in Oregon, U.S.A., and in Costa Rica, Central America. Local species richness was quite variable. Tropical sites did not always have more species nor was there a significant difference in local species richness between regions. However, the species pool for the tropical transects (75) was larger than for Oregon (44). The density of individuals per square meter was much greater in the temperate sites.

Between-habitat diversity differences may account for most of the increase in over-all gastropod species richness in Costa Rica. A regression analysis suggests that, among the variables tested, only the number of gastropod refuges explains a significant amount of the variation in local species richness among all sites.

An increase in carnivorous and carrion-eating snail species accounts for most of the expansion in species richness in Costa Rica. This increase is principally in species that eat different food resources than do temperate zone snails (*e.g.*, sipunculans and small fishes) and species that feed on polychaetes, gastropods, and dead or injured animals.

INTRODUCTION

MANY TAXA OF plants and animals, including gastropods (THORSON, 1952; KOHN, 1971), have an increasing number of species along a decreasing latitudinal gradient (PIANKA, 1966). This ecological phenomenon has been the focus of many studies, and several hypotheses based on physical and biological processes have been developed to explain the generation and maintenance of this pattern (PIANKA, 1966; PIELOU, 1975; HUSTON, 1979).

One interesting question about this diversity pattern is whether specific tropical habitats have a greater diversity than similar habitats in the temperate zone. If so, what ecological processes allow more species to co-occur in the tropical habitats? Are there simply additional, different microhabitats present within these "similar habitats" in the tropics compared to the temperate zone? Are important resources (such as food and habitat) more finely partitioned? Have physical and/or biological disturbances (*i.e.*,

predation) kept species populations reduced in size so that episodes of interspecific competition, if they occur at all, are brief?

The general purpose of this study was to examine quantitatively rocky intertidal areas in Oregon and Costa Rica in order to provide answers to the following questions:

A. How does the gastropod and chiton species richness in rocky intertidal areas differ between temperate and tropical regions of West America?

B. What physical factors might explain some of the variation in species richness between these areas?

C. Do tropical carnivorous gastropods use food resources differently than temperate snails?

SITE DESCRIPTIONS AND METHODS

Table 1 describes the study sites chosen to sample areas with different wave exposures and topographies. The Oregon sites were studied from April to August, during 1970, 1971, and 1972, the Costa Rican sites, in January and February, 1972.

¹ Contribution Number 14.

Table 1

Description of the exposed-coast rocky intertidal study sites in Oregon and Costa Rica.

Locality	Tidal range	Transect name (abbreviation)	General description
Cape Arago, Oregon, U.S.A.	2.1 m	North Cove (NC)	cliff with high splash pool
		Middle Cove 1 (MC1)	ledge area with no loose boulders
		Middle Cove 2 (MC2)	boulder field
		South Cove (SC)	bedrock with ledges and loose boulders
Cape Blanco, Oregon, U.S.A.	2.2 m	Cape Blanco 1 (CB1)	bedrock with ledges and loose boulders
		Cape Blanco 2 (CB2)	bedrock with ledges and loose boulders
Playa Hermosa, Guanacaste, Costa Rica	2.7 m	Playa Hermosa 1 (PH1)	bedrock with ledges and loose boulders
		Playa Hermosa 2 (PH2)	bedrock with ledges and loose boulders
		Playa Hermosa 3 (PH3)	bedrock with ledges
Sámara, Guanacaste, Costa Rica	2.7 m	Sámara 1 (S1)	flat bedrock, ledges, and loose boulders
		Sámara 2 (S2)	flat bedrock, ledges, and much algal turf
		Sámara 3 (S3)	flat bedrock with ledges and tidepools
Quépos, Puntarenas, Costa Rica	2.5 m	Quépos 1 (Q1)	large boulders
		Quépos 2 (Q2)	bedrock with ledges and loose boulders

At each site, I chose a point at the high-tide drift line and placed the base point for a transect a random number (between 0 and 50) of meters from this point along the drift line. I stretched a metric tape from the base point toward the water's edge at low tide and placed quadrats (1 m × 1 m) across the transect line at arbitrarily set intervals according to the length of the transect and the time available to complete the work. For instance, South Cove was sampled every meter along the transect line, while at Sámara 3, the interval was every 5 m. Within each quadrat I counted all snails, chitons, and nudibranchs and noted their positions (under rocks, on top of rocks, etc.). I did not include vermetid snails and octopuses. Due to difficulties in differentiating the numerous small *Fossarus* spp. from the similarly shaped and marked *Littorina aspera* in Costa Rica, I lumped these species. I had similar problems distinguishing *Collisella paradigitalis* from *C. digitalis* in Oregon so I lumped them together. When *Fossarus* spp., *Littorina* spp., and limpets occurred in high numbers, I counted them within six 10-cm² quadrats placed randomly within the 1-m² quadrat and extrapolated their densities to 1 m² from the average of these counts.

I quantified the intertidal height above 0-m low tide at 20-cm intervals on the transect line within each sampled quadrat using a simple surveying technique (placing a pole on the transect line and sighting a horizontal line from a marked position on this pole, a flag on a stationary pole a known distance above the 0-m tide point, and the horizon). Based on C. M. Yonge's method of zonation (RICKETTS *et al.*, 1968), I used 174 cm above mean lower low water (0-m tide) as the separation height between high and mid intertidal zones for Oregon. Since tropical intertidal areas are not as well studied and the tidal datum is different (mean low water spring tides), I based the separation height between high and mid intertidal zones in Costa Rica on gastropod assemblages. I determined it

to be the lowest height reading (120 cm) of the quadrats that contained only those gastropod species (*Littorina aspera*, *L. modesta*, *Nerita funiculata*, *N. scabricosta*, *Planaxis* spp., *Tegula pellisserpentis*, *Purpura pansa*, and *Acanthina brevidentata*) whose distributions are limited to the high intertidal zone and the extreme upper portions of the mid intertidal zone (KEEN, 1971; SPIGHT, 1976; GARRITY & LEVINGS, 1981).

I quantitatively or qualitatively estimated some physical factors that might influence species richness. I qualitatively estimated wave exposure (0.0 = lowest exposure to waves; 1.0 = greatest exposure) for each transect by observing surf conditions and by assessing the number and size of loose rocks. Using the average height measurements for each quadrat, I computed the proportion of quadrats that occurred below the high intertidal zone in each transect (Quépos 1 was excluded due to sampling problems). As a measure of the availability of gastropod refuges, I computed for each transect the proportion of quadrats in which snails were found on the undersides of rocks or ledges.

Since all of the values of these variables vary between 0 and 1, I angularly transformed them before computing a stepwise multiple regression with species richness. I included a latitude variable in this analysis, computed as a ratio of the transect's latitude divided by 90°; I also angularly transformed this ratio.

The diets of the carnivorous and carrion-eating gastropods were determined from a literature review (MILLER, 1974), from field observations, and by collecting individuals in the field, isolating them in containers of sea water for up to 24 h, and then microscopically examining fecal pellets for prey hard parts. I assigned the carnivorous snail species to various diet categories based on the percentage of occurrence of specific food items in their diets. If 75% or more of the food items in a species' diet were in one

Table 2

A comparison of the species richness and density of gastropods and chitons in the Oregon and Costa Rican transects.

	Oregon						Costa Rica							
	NC	MC1	MC2	SC	CB1	CB2	PH1	PH2	PH3	S1	S2	S3	Q1	Q2
Number of quadrats	8	14	14	51	19	13	14	15	13	23	25	32	14	9
Species richness	13	18	28	36	19	22	27	28	15	33	34	29	38	26
$\bar{X} \pm \text{SEM}$			22.7 \pm 3.34							28.8 \pm 2.43				
U-test							N.S.							
Number/m ²	61	83	171	188	143	140	341	47	105	49	28	34	46	18
$\bar{X} \pm \text{SEM}$			131.0 \pm 20.2							83.5 \pm 37.9				
U-test							U = 40, P < 0.05							

diet category, I assigned that species only to that diet category. If less than 75% of the feeding observations were in one category, I assigned the species to the two diet categories that made up at least 70% of the diet. If the two most common diet categories comprised less than 70% of the observations, I included the third highest diet category.

MILLER (1974) lists the chiton and gastropod species discussed in this study as well as their abundances and the diets of the carnivorous and carrion-eating snails. These lists may be obtained from the author. Voucher specimens reside in the author's collection.

RESULTS

Species Richness

The number of species of gastropods and chitons is extremely variable in both Oregon and Costa Rica (Table 2). The number of species found in a local area does not differ significantly between regions. The density of gastropods and chitons is, however, significantly greater in the Oregon transects.

The species pool for the Oregon samples (44) is much smaller than that for the Costa Rican samples (75); thus, there is an increase in the number of gastropod species with decreasing latitude when large geographic areas are considered.

Physical Factors

In an attempt to ascertain what physical factors might explain some of the variation in species richness among the transects, I compiled a list of potentially important variables (Table 3) that I was able to quantify or qualitatively estimate.

I chose wave exposure (WAVES) as a variable since the degree of exposure of an intertidal area to wave shock is important in determining what kinds of organisms occur there (RICKETTS *et al.*, 1968). I picked the proportion of

samples from below the high intertidal zone in a transect (HT) as a variable because there is a trend of increasing species richness with a decrease in intertidal height (JOHNSON, 1970; MILLER, 1974; SPIGHT, 1977). The presence of undersides of rocks, boulders, or ledges increases the topographic complexity of an area and provides microhabitats for the snails that are more sheltered from mortality factors like desiccation and wave shock than areas with only flat bedrock (KOHN & LEVITEN, 1976; MENGE & LUBCHENCO, 1981). For this reason, I calculated a refuge variable (REF) by computing the proportion of quadrats in each transect that had undersides of rocks or ledges occupied by gastropods. I included latitude (LAT) as a variable since it could include some biological and physical parameters that are different in the tropics compared to the temperate zone, but which I did not measure (PIANKA, 1966; HUSTON, 1979).

Although not a physical factor, I also used the number of sampled quadrats (QUADS) as a variable since, at least for Oregon, species richness (S) may be related to it in my study ($S = -8.66 + 25.8 \log \text{QUADS}$; $t = 3.21$, $P < 0.025$; $R^2 = 0.72$). For Costa Rica, none of the regression analyses using log-transformed or untransformed values of S and QUADS resulted in a significant regression or an R^2 value greater than 0.14.

A comparison of each of the variables in Table 3 for a significant difference between Oregon and Costa Rica indicated that only "Latitude" was significantly different ($U = 48$, $P < 0.001$).

I did a stepwise multiple regression using these variables to find out which ones might explain significant amounts of the variation in species richness (S) among all of the transects (excluding Quépos 1). The largest total adjusted R^2 , 0.83, was obtained using the logarithm of species richness; the only significant independent variable was the gastropod refuge variable ($F = 6.0$, $P < 0.05$). The regression equation was: $\log S = 0.004 \text{ QUADS} - 0.003 \text{ LAT} + 0.003 \text{ REF} + 0.001 \text{ HT} - 0.002 \text{ WAVES} + 1.319$.

Table 3

Summary of the physical factor measurements and estimates, the latitudes, and the sample sizes of the Oregon and Costa Rican transects.

Transect	Wave exposure	Proportion of quadrats below high intertidal zone	Proportion of quadrats with gastropod refuges	Latitude	Number of 1-m ² quadrats sampled
Oregon					
North Cove	1.00	0.27	0.00	43.32°	8
Middle Cove 1	0.80	0.38	0.14	43.32°	14
Middle Cove 2	0.40	0.75	1.00	43.32°	14
South Cove	0.40	1.00	0.53	43.32°	51
Cape Blanco 1	0.80	0.70	0.26	42.50°	19
Cape Blanco 2	0.80	0.92	0.54	42.50°	13
Costa Rica					
Playa Hermosa 1	0.60	0.57	0.50	10.50°	14
Playa Hermosa 2	0.60	0.84	0.40	10.50°	15
Playa Hermosa 3	0.80	0.60	0.08	10.50°	13
Sámara 1	0.20	0.89	0.35	9.87°	23
Sámara 2	0.40	0.97	0.60	9.87°	25
Sámara 3	0.20	1.00	0.19	9.87°	32
Quépos 1	0.80	—	0.79	9.45°	14
Quépos 2	0.80	0.94	0.67	9.45°	9

The Between- and Within-Habitat Components of Diversity

Total diversity in a large geographic region consists of two components: within-habitat diversity and between-habitat diversity (MACARTHUR, 1965). If within-habitat diversity has contributed significantly to the larger species pool in Costa Rica, then similar habitats should support more diverse assemblages of gastropods and chitons there than in Oregon. Two lines of evidence in my study suggest that the within-habitat component is not as important as the between-habitat component for rocky intertidal habitats.

First, transects in Oregon and Costa Rica that are similar in wave exposure, proportion of quadrats below the high intertidal zone, and proportion of quadrats with gastropod refuges (Table 3) have similar diversities (Table 2)—*e.g.*, South Cove and Sámara 2; Cape Blanco 2 and Quépos 2. Second, the number of species found in individual 1-m² samples is not significantly different between the two regions ($U = 37.5$, $P > 0.05$). These values ranged from 4.1 to 7.8 ($\bar{X} = 5.8 \pm 0.59$ SEM) in Oregon and from 2.8 to 5.3 ($\bar{X} = 4.4 \pm 0.29$ SEM) in Costa Rica.

Between-habitat diversity appears to be different between regions. To assess this, I compared for each region the percentages of (1) omnipresent species, (2) species found in all transects except one, and (3) species unique to one transect (Table 4). These results suggest that transects in Oregon have more species in common and have fewer unique species. This may mean that the transects

are sampling similar habitats in Oregon and more different habitats in Costa Rica.

Comparison of the percentages of the species in each transect that are also found in one or more other transects (SALE, 1980) also suggests an increase in the between-habitat component in Costa Rica. Oregon transects have significantly greater percentages than Costa Rica ($U = 44.5$, $P < 0.01$). The average percentage is 93.1% for Oregon transects and 88.3% for Costa Rican transects.

Trophic Structure

In the trophic structure analysis, I lumped carnivorous and carrion-eating snails together since I could not tell whether snails known to feed on carrion would also eat living prey. Some snails that normally attacked living prey were observed eating dead animals.

Table 4

A comparison of the percentage of species found in all transects, the percentage in all transects except one, and the percentage unique to one transect.

	Oregon	Costa Rica
% omnipresent	9.1%	2.7%
% in all but one transect	34.1%	10.7%
% unique	29.5%	36.0%

Table 5

Comparison of the trophic characteristics of the assemblage of species in each transect.

	NC	MC1	MC2	SC	CB1	CB2	PH1	PH2	PH3	S1	S2	S3	Q1	Q2
No. herbivorous species	10	12	20	22	12	14	14	17	10	22	21	13	20	13
$\bar{X} \pm \text{SEM}$			15.0 \pm 2.0							16.2 \pm 1.6				
No. carnivorous and carrion-eating species	3	6	8	14	7	8	13	11	5	11	13	16	18	13
$\bar{X} \pm \text{SEM}$			7.7 \pm 1.5							12.5 \pm 1.4				
Proportion of carnivorous and carrion-eating individuals	.06	.03	.03	.06	.06	.05	.07	.37	.05	.15	.33	.54	.27	.28
$\bar{X} \pm \text{SEM}$			0.05 \pm 0.01							0.26 \pm 0.06				

The assignment of some of the grazing mollusks to the carnivorous or herbivorous trophic level is difficult since some species may be indiscriminate grazers, feeding on both plant and animal material. For instance, some species of *Calliostoma* graze on sessile animals (MILLER, 1972; PERRON, 1975); but I did not find animal remains in the feces of seven *C. ligatum* from the Oregon transects. Except for *Placiphorella velata*, which entraps and eats mobile crustaceans (MCLEAN, 1962; Miller, personal observation), most chitons graze on plant material (references in MORRIS *et al.*, 1980). However, there is evidence that some species of *Mopalia* graze on sessile animals and algae (BARNAWELL, 1960). In this study I have considered all chitons except *P. velata* as herbivores, *C. ligatum* as an herbivore, and all species of *Cypraea* as carnivores.

There is no significant difference in the number of herbivorous species found in transects in Oregon compared to Costa Rica (Table 5; $U = 29$, $P > 0.05$). However, Costa Rican transects have significantly more carnivorous and carrion-eating species than Oregon ($U = 38$, $P < 0.05$). The Costa Rican transects also have a larger proportion of carnivorous and carrion-eating individuals than Oregon transects (Table 5; $U = 44.5$, $P < 0.01$). The proportion of carnivorous and carrion-eating species in the species pool is 0.41 in Oregon and 0.52 in Costa Rica.

The Diets of Carnivorous and Carrion-Eating Snails

Since the increase in species richness in Costa Rica occurs primarily in carnivorous and carrion-eating species,

I examined the diets of these snails to compare food-resource use between temperate and tropical species (Table 6). The main differences are threefold increases in the number of snail species eating polychaetes and gastropods in Costa Rica compared to Oregon and the exploitation by tropical snails of sipunculans and fishes, two food types not used by Oregon gastropods.

There is also a large increase in species eating dead material in the tropics, due mainly to the numerous species of Columbellidae. Most columbellids are attracted to dead and/or injured prey (MARCUS & MARCUS, 1962; SPIGHT, 1976; HATFIELD, 1979; Miller, personal observation), but not enough work has been done to show that columbellids are only carrion-eaters.

DISCUSSION

I examined the gastropod and chiton species richness at several similar, exposed-coast rocky intertidal zone sites in Oregon and Costa Rica. Local species richness is quite variable (Table 2). The tropical transects were not always richer nor was there a significant difference in the number of species found in Oregon and Costa Rican transects. However, the density of gastropods and chitons was significantly greater in the temperate areas (Table 2). The total number of different gastropod and chiton species in all Costa Rican transects (75) is much larger than in all Oregon transects (44).

These results agree with SPIGHT's (1977) comparisons of prosobranch species richness at two Washington State rocky intertidal locations and one Costa Rican site. The

Table 6

Number of carnivorous and carrion-eating gastropod and chiton species feeding in each diet category. * Indicates that species exist but were not found in my samples.

	Sponges	Coelen- terates	Sipun- culans	Poly- chaetes	Live, mobile crusta- ceans	Bar- nacles	Bi- valves	Gastro- pods	Bryo- zoans	Echino- derms	Tuni- cates	Fishes	Para- sitic	Dead animals
Oregon	3	2	0	4	1	5	3	1	1	0*	1	0	2	3
Costa Rica	1	1	2	13	0*	7	3	4	0	1	1	1	1	10

difference in the number of tropical prosobranch species in Spight's study (79) and mine (61) may be due to his deliberate sampling of as many habitats as possible at this one site (SPIGHT, 1976, 1977). It is possible that the Cape Arago region in Oregon, where I found 25 prosobranch species, has more habitats than the more wave-protected Puget Sound area (Shaw Island) in Washington, where Spight found 16 prosobranch species.

The between-habitat component of species diversity appears to contribute more than the within-habitat component to the larger total species richness that I found in Costa Rica. This suggests that I was sampling a greater diversity of habitats in Costa Rica and agrees with SPIGHT's (1977) conclusion that there are more niches (defined by substratum and intertidal height) in Costa Rica with no temperate zone counterparts.

Although many different physical and biological factors may control local species richness, the only significant variable of those that I measured or estimated as explaining significant amounts of variation in species richness (Table 3) was the presence of gastropod refuges. The availability of the undersides of rocks and ledges as shelters from wave shock, UV radiation, insolation, desiccation, and large, visual predators has also been found by others to be important in controlling species diversity and population sizes (KOHN & LEVITEN, 1976; JOKIEL, 1980; MENGE & LUBCHENCO, 1981).

The most obvious differences between the trophic structure in Oregon and Costa Rica are the significant increases in the tropical region in the number of species of carnivorous and carrion-eating gastropods and in their proportion of the total individuals. The number of herbivorous gastropod and chiton species per transect is also greater in Costa Rica than in Oregon, but not significantly. Three of the tropical carnivorous snail species use food resources present in the Oregon rocky intertidal but not eaten by Oregon snails (sipunculans and fishes) and a large number (13) prey on polychaetes. There are also substantial increases in the number of snail species eating living gastropods (4) and dead or injured animals (10) in Costa Rica.

Although the more diverse carnivorous gastropod assemblage in Costa Rica has large numbers of species sharing some food resources (at least on a large scale) and other species eating prey not consumed by Oregon species, I do not have enough dietary information to conclude that competition has been more important in structuring the gastropod community in Costa Rica than in Oregon compared to some of the other possible structuring forces, such as predation (MENGE & LUBCHENCO, 1981).

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Range Extensions of Three Opisthobranch Mollusks to the San Diego-La Jolla (California) Ecological Reserve

by

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SINCE JUNE, 1980, we have studied the subtidal fauna (by scuba diving) off La Jolla Shores Beach, La Jolla, California (32°51'–52'N; 117°15'–16'W) in the San Diego-La Jolla Ecological Reserve, within which collecting of any kind is prohibited. The bottom is a sandy habitat that gently slopes to about 12 m, and then precipitously, at 60° to 90° angles, drops into the La Jolla Branch of the La Jolla Submarine Canyon. The cliff faces and ledges of the canyon at 12.2 to 18.3 m consist of soft mudstone. Although this habitat supports a generally depauperate opisthobranch fauna, three of the opisthobranch species observed constitute southward range extensions.

Aglaja ocelligera (Bergh, 1894)

The reported range of *Aglaja ocelligera* (Cephalaspidea: Aglajidae) is from southern British Columbia, Canada, to Santa Cruz Island and Coal Oil Point, Santa Barbara County, California (SPHON & LANCE, 1968, p. 76; SPHON, 1972, p. 55; GOSLINER, 1980; BEHRENS, 1980, p. 32).

The following records from La Jolla Canyon extend the range southward more than 250 km:

- (1) One specimen; 10 mm long, 9.1 m deep; 8 November 1981.

- (2) Three specimens; 15 mm, 18.3 m deep; 16 mm and eggs, 15.2 m deep, inside the stomach of *Astropecten armatus*; and 20 mm, 7.6 m deep; 25 December 1981.
- (3) One specimen; 20 mm, 13.1 m deep; 7 February 1982.

The finding of one specimen inside the sea star *Astropecten armatus* Gray, 1840, is another record of predation upon an opisthobranch, a group considered to have few natural predators. MAUZEY *et al.* (1968) reported that in the Puget Sound region, another sea star, *Crossaster papposus* (Linnaeus, 1767), fed upon *Aglaja diomedea*.

Flabellina pricei (MacFarland, 1966)

The known northern range limit of *Flabellina pricei* (Nudibranchia: Aeolidacea: Flabellinidae) (generic placement follows GOSLINER & GRIFFITHS, 1981) has been expanded from the type locality of Monterey, California (MACFARLAND, 1966, p. 316), to Duxbury Reef, Marin County, California (GOSLINER & WILLIAMS, 1970, p. 177), and to Pearse Island, northern British Columbia, Canada (LAMBERT, 1976, p. 295). Its known southern range limit is Point Fermin, San Pedro, Los Angeles County, California (SPHON, 1972, p. 60).

The following specimens extend its known range southward about 145 km to La Jolla Canyon:

- (1) Three specimens; 17 mm long, 10 m deep; 13 mm, 15.2 m deep; and 18 mm, 8.5 m deep; 14 May 1982.

¹ U.S. mailing address: 416 W. San Ysidro Blvd., K-229, San Ysidro, California 92073.

Cerberilla mosslandica McDonald & Nybakken, 1975

The known distribution of *Cerberilla mosslandica* (Nudibranchia : Aeolidacea : Aeolidiidae) is restricted to the type locality of Monterey Bay, in central California, from 16 to 63 meters of water. The specimens collected by the Moss Landing Marine Laboratory benthic sampling team ranged from 5 to 9 mm in total length when alive.

The following animal seen in the La Jolla Canyon represents a southern range extension of more than 550 km, its first reported occurrence elsewhere than the type locality, a new size record, and a slightly shallower bathymetric distribution:

- (1) One specimen; 18 mm long, 12.2 m deep; 16 July 1982.

ACKNOWLEDGMENTS

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NOTES, INFORMATION & NEWS

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In addition a few comments regarding postal service and the costs thereof seem in order. Because of some distressing experiences with the Postal Service in recent years, we now urge authors who wish to submit manuscripts to our journal to mail them as insured parcels, with insurance high enough to cover the complete replacement costs. If the replacement costs exceed \$400.00, the manuscript should be sent by registered mail with additional insurance coverage (the maximum limit of insurance on parcel post is, at present, \$400.00). We are unable to advise prospective authors in foreign countries and would urge them to make the necessary inquiries at their local post offices.

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A.S.Z.

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There are 15 symposia tentatively planned, several of which may be of interest to our readers. For detailed information contact Mary Wiley, Business Manager, American Society of Zoologists, Box 2739, California Lutheran College, Thousand Oaks, California 91360. Telephone: (805)492-3585.

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b) Books

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c) Composite works

FEDER, H. M. 1980. Asteroidea: the sea stars. *In*: R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal invertebrates of California*. Stanford Univ. Press, Stanford, Calif. pp. 117–135.

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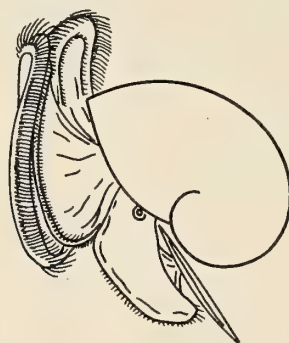
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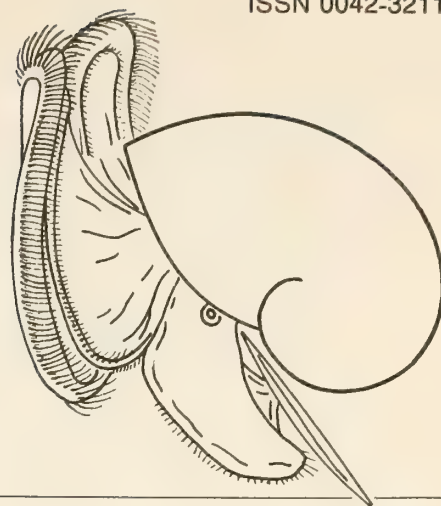
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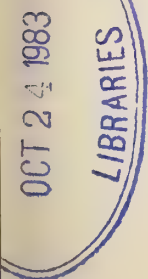
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Radular Patterns, Systematics, Diversity, and Ecology of Deep-Sea Limpets

by

CAROLE S. HICKMAN

Department of Paleontology, University of California, Berkeley, California 94720

Abstract. Sixteen distinct radular patterns from deep-sea limpets are illustrated and discussed. Two of the patterns are docoglossan, nine are rhipidoglossan, and five do not fit the standard classification of gastropod dentition. The diversity of gastropods that have converged on limpet shell form is remarkable. The animals occur in three major deep-sea settings: at hadal depths in eutrophic nearshore trenches; at eutrophic hydrothermal vents at divergent oceanic plate boundaries; and associated with isolated "food falls" in oligotrophic regions of the bathyal and abyssal zone. Many of the taxa are opportunistic specialists on unusual substrates such as wood, sea-grass rhizomes, cephalopod beaks, empty polychaete tubes, and empty skate or shark egg cases. Radular morphology is not, however, convergent in groups that have converged on the same unusual substrates. Different taxa have adopted alternative morphological solutions to using the same substrate. The high diversity of minute limpets in the deep sea today is equalled only by the diversity of minute limpets in the initial Cambrian radiations of the Mollusca. The protective function of limpet shell geometry that is invoked for familiar shallow-water intertidal limpets is not applicable to minute deep-sea limpets or to Cambrian limpets. Freedom to experiment with reproductive and respiratory modes is proposed as an important factor in the evolution of limpet geometry.

Radular characters provide powerful taxonomic tools at the family level, and above, because they reflect fundamentally different groundplans. At the generic and specific levels, however, radular characters must be used with caution because the tendency for morphology to degenerate or fail to develop exceeds evolutionary "perfection" or "fine-tuning" of elaborate structure.

Pseudococculinidae fam. nov. is proposed to provide consistent familial level distinction of groups separated by major discontinuities in radular patterns.

INTRODUCTION

THE TERM "limpet" is applied to a variety of gastropods with low, broadly conical shells. It denotes not only a shell form that has evolved numerous times within the class, but also the accompanying habit of clinging or clamping to rocky substrates (YONGE & THOMPSON, 1976, p. 51). Accordingly, functional interpretations of the limpet shell form have emphasized the theme of protection at the expense of mobility (YONGE & THOMPSON, 1976, p. 265). Protection has been identified as resistance to predation as well as resistance to the physical stresses of the intertidal zone on rocky coasts: notably wave shock, temperature, desiccation, and salinity stress (VERMEIJ, 1978; BRANCH, 1981).

Not all limpets live on rocky substrates, however. The purpose of this paper is to call attention to the extraordinary taxonomic diversity of gastropods that have adopt-

ed this shell form in deep water (below 200 meters). At least 15 families are involved. Many of the deep-sea limpets have minute shells (less than 5 mm long) and are poorly studied anatomically. Examination of their radulae has revealed striking differences within taxa heretofore considered to be closely related. Several of the radular patterns are so unique that they do not fit the standard classification and terminology used to describe gastropod radulae.

Although radular anatomy will contribute substantially to evaluating the taxonomic relationships of deep-sea limpets, comprehensive systematic revision will require a great deal of further study of the soft anatomy. However, it is appropriate at this time to summarize and illustrate the range of radular morphology and correspondingly high diversity of feeding modes in order to stimulate further interest in the biology and systematics of these animals.

Many are restricted to unusual substrates in the deep sea, including water-logged wood, rhizomes of *Thalassia*, empty polychaete tubes, empty skate egg cases, cephalopod beaks, and bone.

There are three major deep settings in which most of the diversity and abundance of limpets is concentrated. None of these settings is typical of the deep sea in terms of the main body of ecological theory concerning this vast portion of the marine realm. The first is the eutrophic nearshore trench or basin that predictably receives large volumes of plant material of terrestrial origin. At low latitudes where trenches border salt marsh or mangrove areas of high productivity, such as the Puerto Rico and Cayman Trenches, the abundance of terrestrial material transported in by turbidity flows may be particularly high (WOLFF, 1976, 1979, 1980; GEORGE & HIGGINS, 1979). The second is the eutrophic setting created by hydrothermal vents, also regions of high productivity, although based on a chemosynthetic rather than photosynthetic pathway (JANNASCH & WIRSEN, 1979, 1981; RAU & HEDGES, 1979; KARL *et al.*, 1980; CAVANAUGH *et al.*, 1981; RAU, 1981). The kinds of limpets that are associated with these first two kinds of food sources are taxonomically distinct. Both groups, however, share opportunistic characteristics that are not normally associated with deep-sea organisms.

Many of the limpets in the first group also occur in a third and more transient setting: as colonists of relatively large "low-quality food falls" (*sensu* STOCKTON & DELACA, 1982) in the form of waterlogged wood that periodically reaches the ocean floor in otherwise oligotrophic regions. The wood-ingesting limpet guild occurs consistently with other invertebrates that also are specialized starting points in the conversion of wood to animal biomass, most notably wood-boring bivalves of the genus *Xylophaga* (TURNER, 1973).

A striking feature of many deep-sea limpets is the small size of the shell. It is potentially of significance to paleontological and malacological debates about the origins and early diversification of the Mollusca. The earliest fossil record of mollusks, not only gastropods but also Monoplacophora and a number of groups of questionable affinities, is dominated by small limpets. Many of these minute forms may have been associated with unusual substrata or may even have lived infaunally. The protective interpretation of shallow-water modern limpet shell form would not apply at this scale. The discovery of a minute (less than 2.5 mm maximum shell length), monoplacophoran limpet associated with small rocks within muddy substrates at the edge of the continental shelf (MCLEAN, 1979) suggests another mode of life—a means of being functionally epifaunal in an infaunal environment. Thus, an analysis of available ecological data on deep-sea limpets and their unconventional substrates provides the basis for some new hypotheses for functional interpretation of the minute limpet form in early mollusks, even though Recent deep-sea limpets are secondarily flattened.

MATERIALS AND METHODS

The following survey of deep-sea limpet radulae is based on extractions from both wet and dry material from numerous sources (see acknowledgments). Dry specimens were rehydrated in saturated trisodium phosphate prior to maceration. Radulae from both wet and dry specimens were removed from the buccal mass following treatment in a 10% solution of sodium hydroxide. All radulae were removed before the buccal mass was completely broken down, so that the chitin of the teeth and radular membrane did not come into direct contact with the caustic solution. Radulae were washed thoroughly in distilled water and dehydrated through an ethanol series from 70% to 100% prior to air drying and mounting for scanning electron microscopic (SEM) examination. Before drying, radulae were cleaned by brief immersion in an ultrasonic cleaner. The intensity of cleaning was based on a combination of the robustness of the radula and its ability to withstand ultrasonication, and the amount of extraneous material on the teeth.

Radulae were manipulated during air drying to expose maximum dentition, which involves laying back the marginal tooth complexes in the rhipidoglossan types. Dry radulae were transferred to SEM stubs and mounted on a thin film of Elmer's Glue[®] thinned with distilled water and allowed to dry until only slightly tacky. It is important not to drop the radula onto wet glue, and even when the glue appears dry, good bonding may be achieved between the radula and the SEM stub by breathing gently on the preparation. All handling of radulae was performed using flexible *minuten nadlen*, extremely fine insect pins, glued to 2-mm-diameter wooden splints.

All specimens were coated with 200–400 Å of gold and viewed at accelerating voltages of 10 kV or less to minimize charging and specimen damage. Preparations illustrating each major radula type were rotated into a standard orientation relative to the electron beam, with the stage maintained flat. The orientation selected allows a diagonal presentation that maximizes areal coverage and resolution. All manipulations were made mechanically with the microscope stage, and not electronically or by scan rotation, to ensure consistent shading. Stereographic pairs were taken of each radula to provide further basis for interpretation. This is particularly important in the analysis of unusual radulae in which the topographic differences between teeth of different types may be considerable, but are not readily perceived, in single electron images.

Scanning electron microscopy is a valuable tool in the study of deep-sea limpet radulae, because their minute size places a great deal of morphological detail beyond the resolvable range of light microscopy. Previous treatments of the taxonomy of deep-sea limpet taxa that include radular data have been illustrated by line drawings that are ambiguous, imprecise, and frequently erroneous in interpretation. The illustrations that follow will help in the

reinterpretation of many drawings in the literature and will enable future workers who do not have access to SEM to interpret light microscope preparations.

The selection of radular material for illustration is made on morphological rather than systematic or typological grounds. The objective is to present the best possible illustration of all the major radular patterns known from the deep sea. In several cases, distinctive patterns are known from a single species and represent the only material available. In most instances, however, the patterns are known from a number of species, and the material illustrated is chosen to show central tendencies and extremes of variation. Because the radulae of type species do not necessarily illustrate central tendencies, they are included only where morphologically appropriate.

RADULAR MORPHOLOGY AND PATTERNS

Fissurellid Limpets (Figures 1, 2, 3)

The keyhole limpets are, as a family, predominantly shallow-water, hard-substrate dwellers. Those forms that do occur in deep water are particularly interesting because their radulae differ from the radulae of shallow-water members of the family, although little is known of their feeding habits or substrate preferences. The radulae of three deep-sea fissurellids are illustrated in Figures 1–3.

Puncturella: *Puncturella* Lowe, 1827 (Figure 1) has the most typically fissurellid radula, and some species in the genus, including the type, *P. noachina* (Linné, 1771), are not restricted to deep water, but occur intertidally in the high latitude portion of their range. The massive, strongly cusped outer lateral teeth and reduced prominence of the rachidian and inner lateral teeth are hallmarks of the fissurellid radula. The radula figured here lacks the pronounced asymmetry that is characteristic of many shallow-water fissurellids (HICKMAN, 1981), but it is not known whether lack of asymmetry is universal in *Puncturella*.

Fissurisepta: *Fissurisepta* Seguenza, 1853 (Figure 2), on the other hand, displays both the prominent outer lateral tooth and the asymmetry. Note that each of the left inner lateral teeth is more anteriorly positioned than the right inner lateral in the same row. This skewing of rows is an accommodation that permits an alternating or zipper-like close-packing arrangement of the large outer lateral teeth when the radula is retracted or folded for storage when the animal is not feeding (HICKMAN, 1981). The combination of serrate cusps on the inner lateral teeth and the absence of both shaft and cusp on the rachidian in this radula is, however, unique.

Zeidora: The radula of the deep-water genus *Zeidora* A. Adams, 1860 (Figure 3) is even more unusual, as judged from examination of one unidentified species. There is no trace of a rachidian tooth, and the outer lateral tooth is of

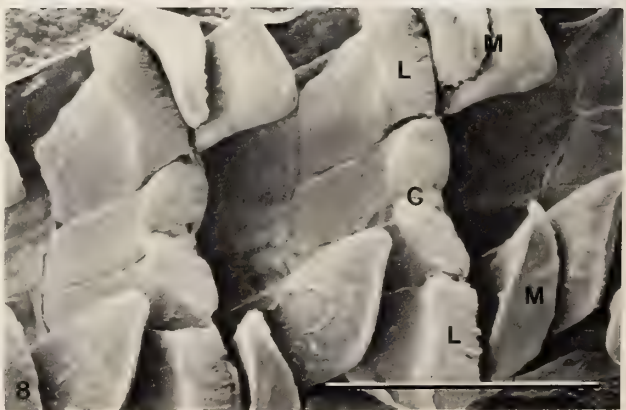
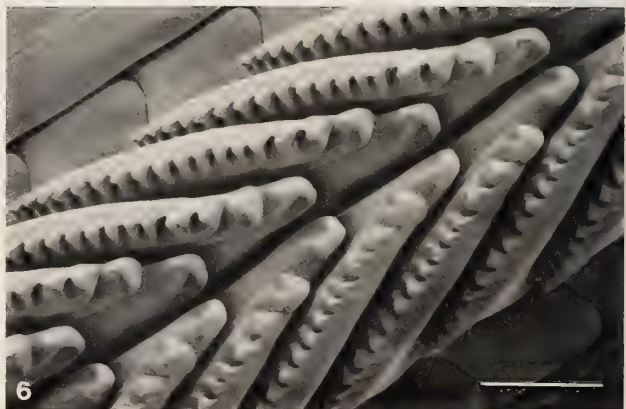
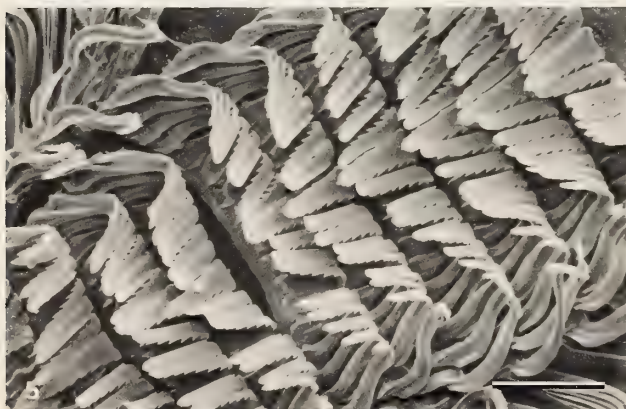
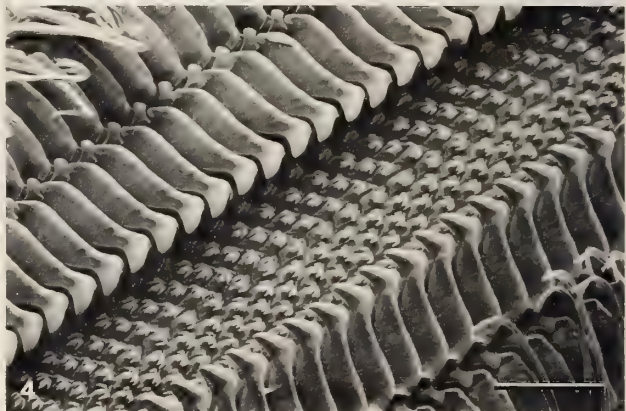
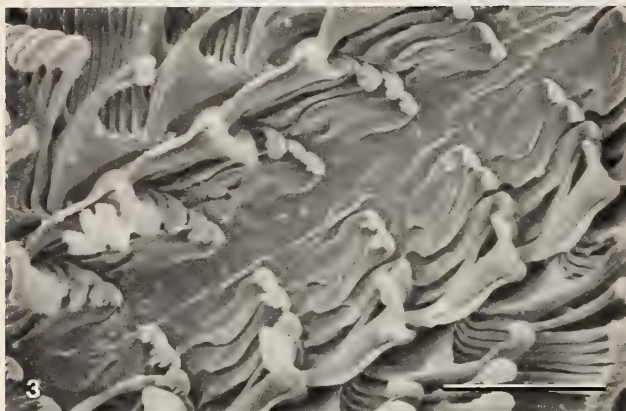
an unusual form in that there is a thin, secondary shaft and cusp that appear to be fused to the main body of the tooth. This suggests that the massive fissurellid outer lateral may, evolutionarily, be a compound tooth resulting from the fusion of what were once distinct elements. The radula is also unusual in that the form of the asymmetry is reversed (*i.e.*, rows are skewed so that the right lateral and marginal teeth fold into the tooth row anterior, rather than posterior to the left lateral teeth in the same row). Based on shell characters, *Zeidora* has been interpreted to be the most primitive genus in the Fissurellidae (FARFANTE, 1947), but the radula of the species investigated is not of a generalized form that would readily permit derivation of other forms of fissurellid dentition.

Limpets Questionably Allied to the Fissurellidae (Figures 4, 5)

Laevinesta: The monotypic genus *Laevinesta* Pilsbry & McGinty, 1952, based on *Nesta atlantica* Farfante, 1947, is so bizarre in its radular morphology that it can no longer be included comfortably in the Fissurellidae, although it may be of fissurellacean derivation (HICKMAN, 1983). The radula (Figure 4) bears little resemblance to that of any living gastropod in its combination of a low central field of teeth with prong-like cusps and its flanking fields of plates. The presence of two, long and slender marginal teeth in each half row does identify it as being of rhipidoglossan derivation, but it is so highly modified and distantly removed morphologically from all other gastropod radulae that it is impossible to ascertain its affinities. The fragile shell is wholly internal, but has a marginal slit and selenizone that are of fissurellid appearance. The animal occurs on sponges and presumably feeds upon them, although the precise nature of the association is not documented.

The generalized form of the radula of *Laevinesta*, in which fields of robust plates replace normal teeth, represents a grade of radular morphology that has been attained independently in several other major groups of deep-sea limpets (*e.g.*, Bathysciadiidae, Addisoniidae) that are associated with unconventional substrates.

Galápagos Rift slit limpet: Another small, emarginate, slit limpet that has a shell of fissurellid appearance occurs at deep-sea hydrothermal vents in the Galápagos Fracture Zone, where it has been recovered from washings of larger sessile mega-invertebrates (ANONYMOUS, 1980). The shell is unusual in that it is asymmetric, with the slit and selenizone forming an acute angle with the line bisecting the shell. It is the radula (Figure 5) that leads to serious questions about the affinities of the animal. It is rhipidoglossan, but there is no asymmetry, no enlarged outer lateral tooth, and no reduction of the prominence of the central tooth field. In fact there is an abnormally high number of lateral teeth (9 per half row in contrast to the traditional 4 of the fissurellid radula). There are other



peculiarities of the radula that will be discussed in greater detail by Turner and Hickman (in preparation).

Patellacean Limpets (Figures 6, 7, 8)

Patellacean limpets, like fissurellids, occur primarily in rocky intertidal habitats, with several offshoots that are specialized for life in the deep sea: notably *Pectinodonta* Dall, 1882, in the Acmaeidae, and *Propilidium* Forbes & Hanley, 1849, *Bathylepeta* Moskalev, 1979, and other members of the family Lepetidae. Deep-sea patellaceans have radulae that are at once recognizable under the light microscope as docoglossan, a highly specialized form of gastropod dentition in which a few, heavily cusped teeth appear brown or black pigmented, due to the addition of iron salts that substantially increase tooth hardness. The radulae of deep-sea patellaceans do, however, contain some peculiarities that are related primarily to fusion of elements.

Pectinodonta: This genus comprises a small, but widely distributed, group of deep-sea species that are primarily members of the wood-ingesting guild. They are frequently recovered from wood (WOLFF, 1979; personal observation) that they cohabit with both cocculinid and pseudo-cocculinid limpets. The radula of *Pectinodonta* (Figure 6) is unusual in the elongation of the third lateral tooth into a multicusped, curved, serrate unit that compresses the first and second lateral teeth, which form, along with the third lateral, a curved diagonal cutting edge with an appearance similar to that of a wood rasp (SCHOOLEY *et al.*, 1982; HICKMAN, 1982). The teeth are set at a steeply acute angle to the longitudinal axis of the radula. Although each pair of compound cutting edges appears to be identical with the pairs anterior and posterior to it, careful inspection of Figure 6 shows that pairs are not strict mirror images and that one tooth set in each pair lies either slightly anterior to or slightly posterior to the other. There is an alternation along the length of each half row of the radula in anterior *vs* posterior placement.

WOLFF (1979) has reported scars on wood from which *Pectinodonta* has been recovered. These probably represent homing depressions produced as a result of activity distinct from feeding. The plane of the aperture is not flat in some species but curved, presumably to conform to a curved, wood surface.

CHRISTIAENS (1979) reviewed the species of *Pectinodonta* and concluded that, because of the close similarity of shell form with that of some cocculinid limpets, some species originally assigned to *Cocculina* are actually *Pectinodonta*. However, LINDBERG (1979) has noted that, even without animals and radulae, the genera are easily separated by major differences in shell structure.

Lepetid limpets: Although the family Lepetidae is by no means restricted to deep water, the comprising species are predominantly subtidal in habit and restricted to cold water, primarily at high latitudes, where they occur on pebbles and cobbles at the sediment-water interface (YONGE, 1960). The ctenidium is lacking (lost?) in lepetids, but without development of secondary gills, which YONGE (1960) has interpreted as requiring continuous submergence while freeing the animal for life on muddy substrates, an impossibility for so many gastropods that face the problem of sediment clogging of the respiratory apparatus. Although no firm evidence supports YONGE's scenario for the evolution of the situation in which specialized respiratory structures are lacking (the *absence* of morphology is always difficult to interpret), a number of unrelated deep-sea limpet groups discussed below also lack ctenidia or secondary gills. MOSKALEV (1977) has described species of Lepetidae that are restricted to deep-sea trenches at depths in excess of 5000 m.

Little is known of the diet of lepetids. YONGE (1960) has observed that *Lepeta* (*Cryptobranchia*) *concentrica* (Middendorff, 1847) feeds on organic detritus that settles out of the water column. The lepetid radula is complicated, and drawings in the literature, although sometimes meticulous (MOSKALEV, 1977), are difficult to interpret. For comparative purposes it is particularly important to

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Explanation of Figures 1 to 8

Figure 1. *Puncturella* sp. Zoological Museum, University of Copenhagen, Galathea Station 436. Bar = 100 μ m.

Figure 2. *Fissurisepta granulosa* Jeffreys, 1882. Specimen provided by A. Warén; Biological Station, University of Bergen Reference Number E39-71. Bar = 20 μ m.

Figure 3. *Zeidora* sp. U.S. National Museum (USNM) 761482. Bar = 40 μ m.

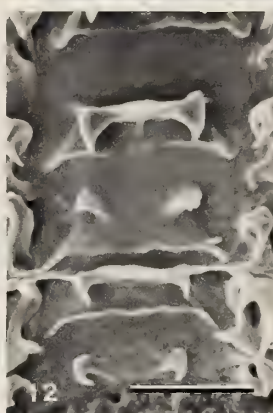
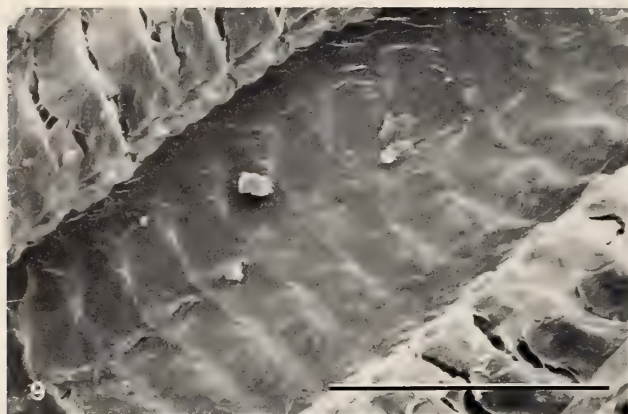
Figure 4. *Laevinesta atlantica* (Farfante, 1947). USNM 792397. Bar = 100 μ m.

Figure 5. Galápagos Rift slit limpet, gen. et sp. nov. Deep Sea Research Vessel (DSRV) Alvin Dive 733. Bar = 40 μ m.

Figure 6. *Pectinodonta* n. sp. U.S. Fish and Wildlife Service Bureau of Commerical Fisheries, R/V Oregon II, Station 11230. Bar = 100 μ m.

Figure 7. *Lepeta* (*Cryptobranchia*) *concentrica* Middendorff, 1847. University of California Museum of Paleontology (UCMP) 2896. Bar = 100 μ m. Dentition from posterior portion of radula. Note the central and lateral teeth are still fused into a single unit that is beginning to separate medially.

Figure 8. *L. (C.) concentrica*. Dentition from the anterior end of the same radula illustrated in Figure 7. Note that the laterals are distinct and separate from the double central tooth. C = central; L = lateral; M = marginal. Bar = 100 μ m.



view the radula at a standardized point in ontogeny due to variation in the amount of fusion of elements along the length of the membrane. This is illustrated by two views of the radula of *L. (C.) concentrica*: in Figure 7, the positionally central and lateral teeth are fused into a single element, although they are beginning to separate medially; and the marginal teeth are separate and fully formed. These teeth are from the posterior portion of the radula. In Figure 8, from the anterior end of the same radula, the teeth are fully formed and worn from use; and the central tooth is double and flanked by worn lateral teeth as well as by worn marginals.

Although I have not been able to examine the radulae of any of the deep-sea lepetid species, drawings in the literature (e.g., MOSKALEV, 1977; DELL, 1956) suggest a basic plan of dentition comparable with that of the shallow-water species discussed above and illustrated in Figures 7 and 8.

Bathysciadiid Limpets (Figures 9, 37a, b)

The family Bathysciadiidae Dautzenberg & Fischer, 1901, and the genus *Bathysciadium* Dautzenberg & Fischer, 1901, were originally based on specimens of a minute, deep-water Atlantic limpet recovered from several stations in the vicinity of the Azores on the remains of cephalopod beaks. The type species, *B. conicum* Dautzenberg & Fischer, 1901, was originally described as *Lepeta costulata* Locard, 1898, and the type is thus a synonym of *B. costulatum*.

The radula of the type species, as drawn by PELSENEER (1901), who described the anatomy from material supplied by Dautzenberg and Fischer, is clearly unusual in form and difficult to interpret. Although PELSENEER concluded that the species was a patellacean limpet, the radula is not docoglossan, nor can it be derived from a docoglossan form of dentition.

Minute limpets subsequently recovered from cephalopod beaks in deep water in both the eastern and western Pacific and depicted as having radulae of similar config-

uration have been assigned not only to *Bathysciadium* (DALL, 1908; THIELE, 1908) but also serve as type species for the genera *Bonus* Moskalev, 1973, and *Bathypelta* Moskalev, 1971. On the grounds that specimens have been reported with and without gills and with one and two kidneys, MOSKALEV (1971) distinguished two families (Bathysciadiidae and Bathypeltidae) and two superfamilies (Bathysciadoidea and Bathypeltoidea), both allied with the docoglossan limpets (MOSKALEV, 1971, 1973, 1978).

The literature treating the anatomy of *Bathysciadium* and its allies is written in four languages (English, French, German, and Russian), and reconciliation of existing differences of opinion is hampered not only by language difficulties but also by the fact that no one has yet been able to compare the anatomy of specimens from the Atlantic and Pacific.

The extraordinary radula of *Bathysciadium pacificum* Dall, 1908 (Figure 9) does not fit any of the major radula types described to date and is so highly modified that it is not possible to determine the type of radula from which it is derived. There is a broad central portion of radular membrane that is without teeth. This region is flanked by two elevated, lateral columns of heavy plates that are interlocked or partially fused, both within rows and within columns, to form continuous, flexible, jointed pavements. A great deal of topographic relief is revealed in paired stereomicrographs of the pavements (Figures 37a, b). There are four plates in each half row: a small inner plate that forms a steep inner wall and partially underlies the adjacent plate; two larger, broadly rectangular plates that are most elevated at the joint between them; and a small, but heavy, outer plate that is squarish in outline, but with a strong elevated ridge parallel to the column axis that divides the plate into steeply-inclined inner and outer faces.

On the basis of the inferred striking similarity of radular configuration and ecological association with remains of cephalopod beaks, it seems probable that the forms described to date are very closely related and may not merit taxonomic distinction of the magnitude proposed by MOSKALEV (1971, 1973). The radula is neither rhipido-

Explanation of Figures 9 to 17

Figure 9. *Bathysciadium pacificum* Dall, 1908. Los Angeles County Museum of Natural History (LACM) 66-152. Bar = 100 μ m.

Figure 10. *Addisonia paradoxa* Dall, 1882. USNM 181201. Bar = 40 μ m.

Figure 11. *Lepetella tubicola* Verrill, 1881. USNM 153171. Bar = 40 μ m.

Figure 12. *L. tubicola*. Detail of newly forming rachidian teeth from posterior end of same radula illustrated in Figure 11. Bar = 20 μ m.

Figure 13. *Addisonia paradoxa*. Enlargement of the outer two

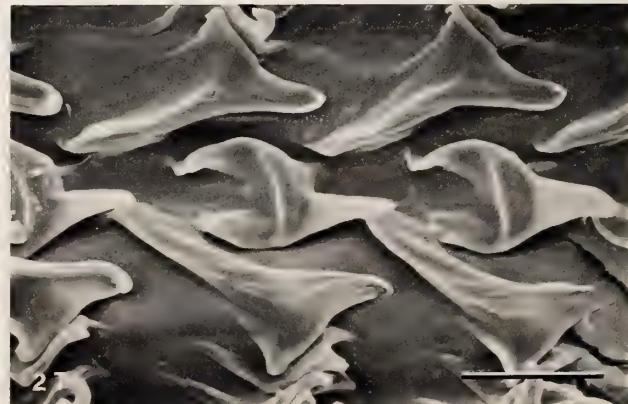
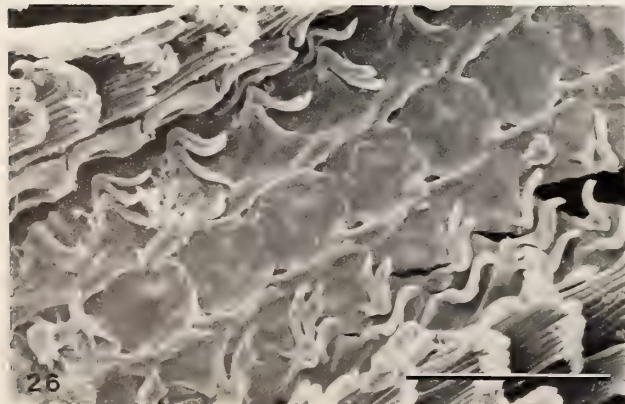
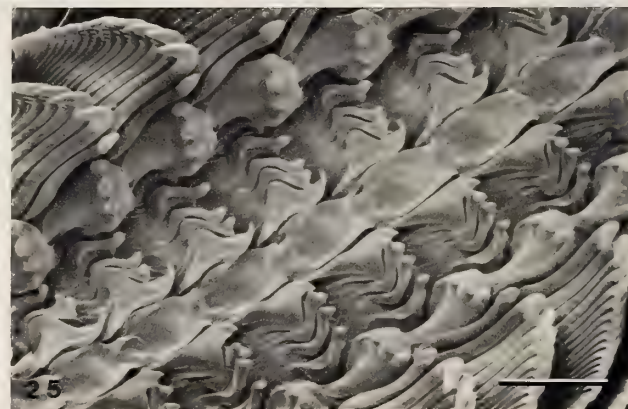
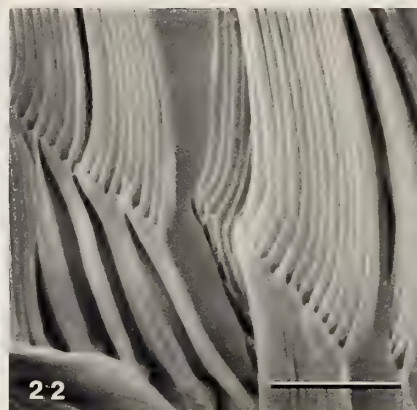
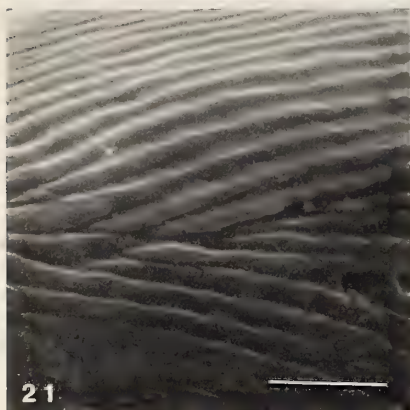
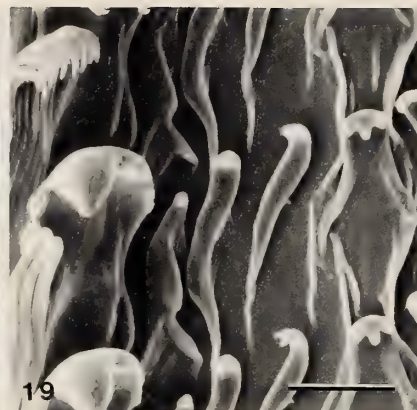
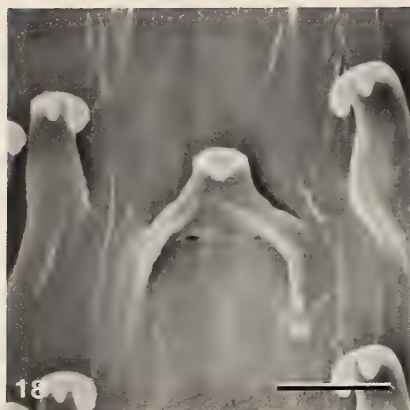
heavily cusped radular plates from same radula illustrated in Figure 10. Structure at arrow may be a degenerate marginal tooth. Bar = 20 μ m.

Figure 14. *Cocculina* sp. A. Zoological Museum, University of Copenhagen, Galathea Station 65. Bar = 40 μ m.

Figure 15. *Cocculina* sp. B. U.S. Fish and Wildlife Service Bureau of Commercial Fisheries, R. N. Oregon II, Station 11220. Bar = 40 μ m.

Figure 16. *Cocculina* sp. C. LACM, uncataloged. Bar = 100 μ m.

Figure 17. *Cocculina* sp. D. Zoological Museum, University of Copenhagen, Galathea Station 276. Bar = 40 μ m.



glossan nor docoglossan, and determination of the systematic position of the Bathysciadiidae and resolution of discrepancies in the literature await careful examination and comparison of the soft anatomy of the constituent species.

Although the substrate of these limpets is potentially difficult to locate and colonize, it is now known that the beaks of cephalopods may form extensive and dense, but highly localized, accumulations at abyssal and hadal depths. BELYAEV (1966) has estimated that they exceed 1000 per m² over extensive areas. Beaks that have been occupied by bathysciadiid limpets are extensively pitted and scarred. There is one species of cocculinid limpet that also lives on cephalopod beaks in the lower abyssal zone, described by MOSKALEV (1976) as *Teuthirostria cancellata*. Although cocculinids normally live on wood, the radula of the cephalopod-beak species is typically cocculinid and is in no way convergent with the bathysciadiid radula.

Addisoniid Limpets (Figures 10, 13, 38a, b)

The genus *Addisonia* Dall, 1882, includes small, deep-sea limpets with thin, markedly asymmetrical shells and a series of anatomical and radular peculiarities that warrant distinction as a separate family, as recognized by DALL (1882). The anatomy is, however, incompletely described (DALL, 1882; VERRILL, 1884; THIELE, 1908), and requires further detailed study to clarify the affinities of the family.

The radula (Figure 10), like that of bathysciadiids, consists of a pavement of radular plates rather than distinctly cusped teeth, although there is no relationship between the plate patterns that would suggest any commonality of descent. It is neither rhipidoglossan nor docoglossan in form, unless one wishes to interpret the outermost element (see arrow in Figure 13) as a degenerate rhipidoglossan

marginal. The number of elements in each transverse row is 15, as interpreted by MOSKALEV (1971, p. 59), although the base number is not clear in the ambiguous series of drawings in the literature (e.g., VERRILL, 1884, pl. 29, fig. 14; THIELE, 1908, pl. 1, fig. 9; DALL, 1889, pl. 25, fig. 1e); and the shapes of individual elements cannot be determined accurately from light microscopy because of their minute size and overlap.

Stereographic-paired, scanning electron micrographs (Figures 38a, b) clarify relationships in the addisoniid radula. The rachidian is a well-developed, subcylindrical element that fits together with the rachidian elements anterior to and posterior to it to form a continuous, jointed, cylindrical column along the central longitudinal axis of the radula. The rachidian is flanked on either side by a pair of solid plates of rhomboidal outline, which are in turn flanked by a pair of small, narrow plates of sigmoid outline. The outermost elements in each half row are two complexly interlocked and heavily cusped plates that are elevated above the remainder of the radular ribbon and a narrow, elongate element that may represent a degenerate marginal tooth shaft. Nothing is known of the substrate preference of the type species (*Addisonia paradoxa* Dall, 1882) but specimens of an *Addisonia* from the eastern Pacific were extracted from inside of a skate egg case (J. H. McLean, written communication, 1983).

Lepetellid Limpets (Figures 11, 12, 39a, b)

Another group of minute, deep-sea limpets with a unique radular pattern and unique substrate association is the family Lepetellidae Dall, 1882, typified by *Lepetella* Verrill, 1880. The Atlantic type species, *L. tubicola* Verrill, 1880, occurs consistently on and in the tubes of the cosmopolitan polychaete genus *Hyalinoecia* Malmgren,

Explanation of Figures 18 to 27

Figure 18. Detail of rachidian tooth from cocculinid radula in Figure 15. Note that the cusp is triangular and undivided. Bar = 10 μ m.

Figure 19. Detail of rachidian and left lateral teeth from cocculinid radula in Figure 14. Note that rachidian cusp is 5-pronged. Bar = 20 μ m.

Figure 20. *Cocculina* sp. E. Australian Museum C.108570. Note the great length and complex morphology of the massive outer lateral tooth and the flattening of marginal tooth shafts. Bar = 40 μ m.

Figure 21. Enlargement of the surface of the cusp of the massive cocculinacean outer lateral tooth illustrated in Figure 20, with its unusual divaricate surface sculpture. Bar = 4 μ m.

Figure 22. Enlargement of cocculinacean marginal tooth shafts from the radula illustrated in Figure 15 and showing prominent flexure at mid height. Bar = 10 μ m.

Figure 23. *Fedikovella caymanensis* Moskalev, 1976. Zoological Museum, University of Copenhagen, ex Akademik Kurchatov Station 1189. Bar = 40 μ m.

Figure 24. *Pseudococculina* sp. A. Zoological Museum, University of Copenhagen, ex Akademik Kurchatov Station 1267. Note the particularly well-developed rachidian. Bar = 40 μ m.

Figure 25. *Pseudococculina* sp. B. Australian Museum 79-05-07. The rachidian is a robust plate lacking the shaft seen in Figure 24. Note strong development of cusps on the large outer lateral. Bar = 40 μ m.

Figure 26. *Caymanabyssia spina* Moskalev, 1976. Although poorly developed, this is recognizable as pseudococculinid dentition. Bar = 40 μ m.

Figure 27. *Pseudococculina* sp. C. Zoological Museum, University of Copenhagen, Galathea Station 664. Bar = 20 μ m.

1867 (VERRILL, 1880; DALL, 1882, 1889; MOSKALEV, 1978). Minute limpets have also been removed from *Hyalinoecia* tubes from deep water off New Zealand. They were originally described by SUTER (1908) as *Cocculina clypidellaeformis*, but FINLAY (1927) subsequently designated this species as type species of the genus *Tectisumen*. Although the affinities of many monotypic, or allegedly monotypic, austral gastropod genera have not been resolved, radular preparations from the type species of *Tectisumen* Finlay, 1927, and *Tecticrater* Dell, 1956, have revealed dentition of the same pattern as *Lepetella tubicola*.

Although VERRILL (1880) described the radula of *Lepetella tubicola* as taenioglossate, this radula provides another example of dentition that does not fit the standard radular classification employing "glossate" terminology. The positionally central tooth of *L. tubicola* (Figure 11) is broad, with a pair of lateral cusps that may result from fusion of once distinct lateral teeth. Fusion is suggested by the pattern of ontogenetic development (Figure 12), in which the earliest stage is the appearance of two cusps separated by a space on the radular membrane. There are three additional elements in the lepetellid radula: a small, free-standing inner lateral tooth with a robust, curved, and inward-pointed cusp, and a massive, tricusped outer lateral that is closely articulated with a large marginal plate. The marginal plates are of an unusual broad and flattened form, and they interlock with one another as well as with the bases of the massive outer laterals. Each plate has four interactions: one each with the plates anterior and posterior to it, and one each with the posterior and anterior basal faces of adjacent outer lateral teeth. Paired stereo-micrographs (Figures 39a, b) demonstrate that the plates are not elevated pavements analogous to those of *Bathysciadium*, *Addisonia*, or *Laevinesta*, and they are inferred to function solely in mechanical adjustments of the inner laterals rather than in food preparation and collection.

Cocculinid Limpets (Figures 14–23)

Cocculinid limpets are small-shelled (usually less than 5 mm maximum length) wood-ingesting gastropods with minute radulae that have been difficult to evaluate with light microscopy. Although two major genera are traditionally assigned to the family (KNIGHT *et al.*, 1960; MOSKALEV, 1971, 1976), *Cocculina* Dall, 1882, and *Pseudococculina* Schepman, 1908, the radulae in these two genera are of radically different plans that require the recognition of separate families (HICKMAN, in press).

The cocculinid radula has many features that make it easy to recognize. Figures 14–17 illustrate a range of variation in this plan. The rachidian tooth ranges from well-developed and cusped (Figure 14) to completely absent, leaving a gap on the radular membrane (Figure 17). Like many presence/absence characters, however, taxonomic significance should not be attached to this. Note that in Figure 15 these two character states exist along the length

of the same radula. Although the rachidian forms initially in some species, it frequently is lost from the anterior half of the membrane. When present, the rachidian consists of two basal limbs that resemble the shafts of lateral teeth that fuse medially to form a short shaft and cusp (Figure 18). The cusp may be entire and bluntly triangular (Figure 18) or subdivided into 3–5 secondary cusps (Figure 19).

There are always three inner lateral teeth of similar morphology (Figure 19), with long, slender shafts and small, coarsely divided cusps. The robustness of the inner lateral teeth is variable, but robust laterals are not positively correlated with the presence of a well-developed rachidian, as illustrated in Figure 16. This radula is particularly interesting because there appear to be four well-developed, lateral tooth shafts. The tops of the inner pair of shafts in each row appear to be broken off, which could be interpreted as failure to fuse and form a rachidian.

The largest and best developed tooth in the cocculinid radula is the massive outer lateral (Figures 19, 20), with a large primary cusp and a smaller secondary cusp on either side. The surface of the primary cusp is not smooth, but bears a unique pattern of divaricate wrinkles (Figure 21). These massive, major food-preparing teeth fold together in alternating zipper-like fashion when the radula is enrolled during retraction at the end of the feeding stroke and for storage within the radula sac (HICKMAN, 1981). Because of the size of the outer lateral tooth, the cocculinid radula provides a classic example of lack of coincidence of what HICKMAN (in press) calls "base rows" and "cusp rows." That is to say that the cusp of the outer lateral is in a row of cusps that is different from the row of bases, making for a much more complex form of functional integration of tooth interactions than is possible in the standard rhipidoglossan radula where base and cusp rows coincide.

The marginal teeth in the cocculinid radula are also unique. The innermost marginals have greatly expanded and flattened shafts that narrow distally to disproportionately tiny, but strongly hooked, cusps. The outer marginals retain this same basic form, with strong lateral flattening of the shafts, but the shaft develops a peculiar twist at mid-length (Figure 22) that is of a design that would facilitate rotation in the upper shaft while the lower shaft remains stationary. There also appears to be a tendency for lower shafts to become fused below the twist. These teeth are extraordinarily long, and like the massive outer lateral, the cusp rows and base rows do not coincide.

MOSKALEV (1976) described six new cocculinid genera based on abundant material collected from abyssal and hadal depths on eight Soviet expeditions. Four of the genera are based on species with pseudococculinid radulae, and these will be discussed in the following section. The other two, *Fedikovella* and *Teuthistroia*, have typical cocculinid radulae. I have examined the radula of *Fedikovella caymanensis* from a specimen collected on the Akademik Kurchatov Expedition (Figure 23) and do not feel that it

is sufficiently different to warrant separate generic recognition. MOSKALEV based the new name on the tridentulate condition of the rachidian, but, as discussed above, the condition of the rachidian in cocculinids is more a result of how faithfully the instructions are carried out in forming the tooth rather than any major variation in the nature of the instructions. *Teuthirostria cancellata* Moskalev, 1976, from the Peru-Chile Trench, is an interesting cocculinid because it occurs on squid beaks, along with *Bathysciadium*, rather than on wood. There is, however, no sign of any convergence on bathysciadiid radular morphology.

DALL (1889) proposed *Coccopygia* for *Cocculina spinigera* Jeffreys, 1883, on the basis of the absence of epipodial tentacles. *Coccopygia* is, however, a preoccupied name, and the radula of *C. spinigera* is not distinct from that of other species of *Cocculina* (based on SEM examination of radulae from USNM 177890). *Maoricrater* Dell, 1956, which has been placed in the Cocculinidae (KNIGHT *et al.*, 1960), has a docoglossan radula and belongs in the Lepetidae. The animal and radula of *Notocrater* Finlay, 1927, are not known, and it too may be a lepetid.

Detailed studies of the anatomy of the cocculinids are badly needed in order to establish the systematic position of these minute rhipidoglossan limpets and their relationships to other deep-sea families. The only account of the internal anatomy of a cocculinid is that of THIELE (1903), who concluded that their closest affinities were with the Neritacea.

Shell morphology of the cocculinids likewise stands in need of review. Although the apex of the shell is posteriorly directed in all species, it varies in placement from far posterior to central; and the shell may be tall and narrowly conical or extremely flattened. Shell surfaces vary from smooth to highly ornamented and pustulose. However, shell surfaces are frequently badly corroded when they reach the surface; and specimens that have been kept in formalin or alcohol for long periods seem to be particularly susceptible to disintegration. Shells are best preserved dry, after being separated from animals that are to be preserved wet. Occasionally, fresh specimens preserve extraordinarily elaborate spinose periostracum (LIPPS & HICKMAN, 1982, fig. 14-13).

Pseudococculinid Limpets (Figures 24–28, 40a, b)

Pseudococculinidae *fam. nov.*: *Pseudococculina* and a group of allied small deep-sea limpets share a plan of radular morphology that is so distinct from that of the Cocculinidae as to warrant separate familial recognition. The details of this plan are described below. The morphological differences require fundamentally different patterns of movement and mechanical interactions of teeth within and between rows that are discussed elsewhere (HICKMAN, in press).

Pseudococculinid limpets also occur on wood, and have

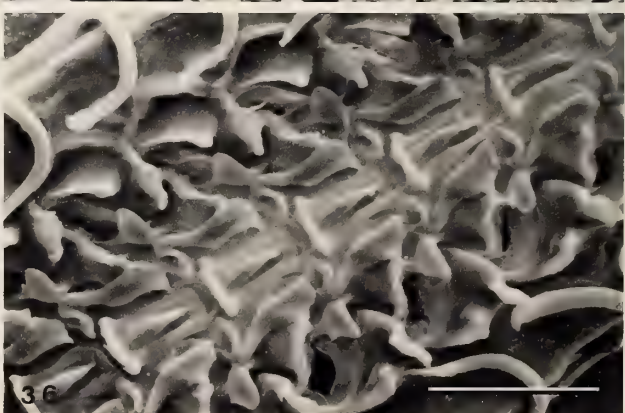
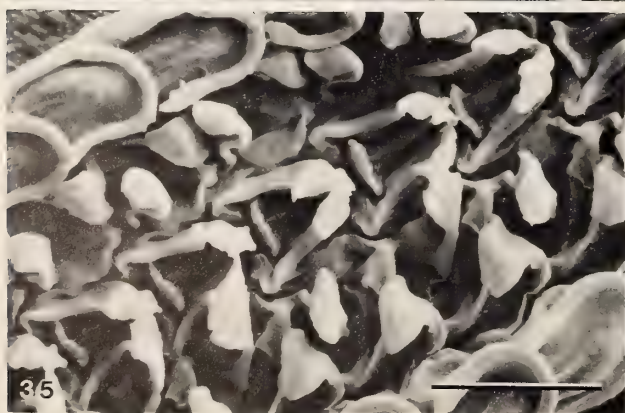
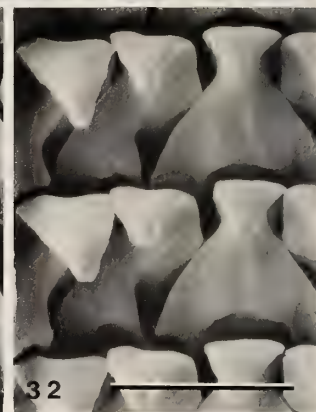
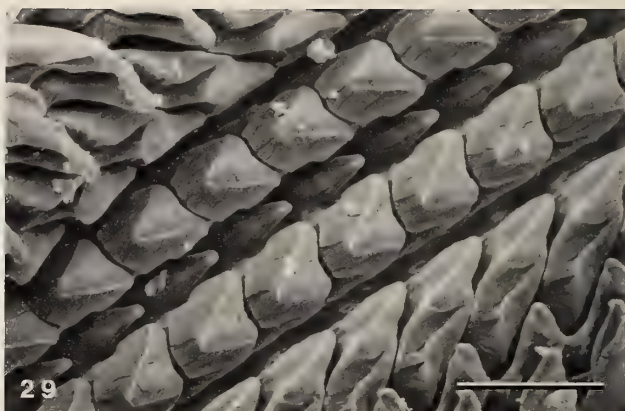
shells and animals that are similar to cocculinid limpets. SCHEPMAN (1908) proposed the genus *Pseudococculina* on the basis of the unique radula of *P. rugosplcata* and *P. granulata*. Although SCHEPMAN (p. 16) noted the presence of a “plumate gill” in the type species, it is absent or poorly developed in pseudococculinids I have examined. As noted earlier, presence or absence of well-developed respiratory organs does not seem to be of profound taxonomic significance in deep-sea limpets, although the nature of the respiratory structures, when present, can be diagnostic. There are no published accounts of the internal anatomy of *Pseudococculina*, and detailed histological comparisons with other deep-sea limpets will be required in order to establish relationships.

The pseudococculinid radula is, like the cocculinid radula, so small that light microscopy has not been adequate to diagnose it. It is superficially similar to the cocculinid radula in the parallel trends toward degeneration of teeth in the central field (particularly the rachidian) and the elaboration of the outer lateral tooth as the major food-preparing structure, accompanied by the development of radular asymmetry.

Figures 24–26 illustrate a range of variation in pseudococculinid radular morphology. The rachidian varies from an asymmetric element with a prominent horseshoe-shaped base and thinner, irregular, tapered extension that cannot be differentiated into shaft and cusp (Figure 24) to a thin, squarish or oval plate (Figure 26). The intermediate condition (Figure 25) frequently involves the development of a plate with thickened edges and irregular or ragged edges or extensions. The degree of development of the rachidian may vary along the length of a single radula, as illustrated in Figure 27.

In contrast to the cocculinid condition, there are four, rather than three, inner lateral teeth in the pseudococculinid radula. The innermost lateral (Figure 27) is an unusual, large, triangular element with a long, inner basal limb and shorter, outer basal limb that fits into a curved pocket on the small second lateral. Figure 27 also illustrates the strongly asymmetric placement of these large teeth on either side of the rachidian. The second, third, and fourth laterals are all strongly curved elements that have small, simple, distal cusps and are designed to interlock closely when the radula is tightly enroled. The outer lateral (fifth lateral) is a massive tooth with a thickened quadrate shaft with a deep pocket on the inner surface that fits over the smaller inner lateral teeth when the radula is not in use. The massive cusp is subdivided into four blunt, terminal denticles. Unlike the massive outer lateral in *Cocculina*, it is a short tooth, and its base and cusp coincide with the bases and cusps of adjacent inner lateral teeth.

The marginal teeth (Figure 28) have short, thick shafts in contrast to the extreme flattening of the elongate and twisted shafts of cocculinid marginals. The shaft thickening is most pronounced in the inner four or five marginals, which also have long, curved, and sharply pointed



cusps. Outer marginals do, however, develop flattened shafts, and the cusps are complexly serrate.

A stereographic pair of the pseudococculinid radula (Figures 40a, b) demonstrates the extreme difference in topography between the massive outer lateral and marginal complex and the poorly-developed central field of teeth.

MOSKALEV (1976) described four genera that I believe to be simple variations on the basic pseudococculinid plan: *Kurilabyssia*, *Caymanabyssia*, *Bandabyssia*, and *Tentaoculus*. MOSKALEV's drawings of the radulae (fig. 1, p. 10) do indicate differences, but the differences seen in light microscopic observations and drawings have to do with degree of development rather than fundamental differences in plan. The radula of *Caymanabyssia spina* (Figure 20) represents the extreme case of not only an underdevelopment of the plate-like rachidian, but also failure to develop the inner lateral tooth except in outline and slight thickening.

MOSKALEV (1976) notes that *Tentaoculus perlucida* has eyes, a feature that is lacking in other pseudococculinids as well as cocculinids, addisoniids, and bathysciadiids. It may be that there will be suites of anatomical differences in many of the deep-sea limpet families that will justify separate generic categories.

Pseudococculina is sometimes extremely abundant on pieces of wood. MOSKALEV (1976) recovered 204 specimens of *Caymanabyssia spina* from a piece of wood 800 mm × 150 mm in size, and large numbers of an undescribed species of *Pseudococculina* have been recovered from wood from deep-sea samples off the east coast of Australia (personal observation).

Bathyphytophilid Limpets

Wood is not the only form of plant material that reaches the deep sea floor in large quantities. There has been a

great deal of interest in recent years in the export of organic matter from high productivity sea-grass beds along the continental margins; and it has been established that this material is transported by turbidity flows and accumulates in deep-sea trenches. It is particularly abundant in the Puerto Rico and Cayman Trenches, where blades and rhizomes of *Thalassia testudinum* comprise 80–90% of the plant material (MENZIES *et al.*, 1967; MENZIES & ROWE, 1969; WOLFF, 1976, 1979, 1980; GEORGE & HIGGINS, 1979). It is, therefore, not extraordinary that there should be communities of deep-sea organisms specialized for using sea grasses as a food source. MOSKALEV (1978) based the family Bathyphytophilidae on a species of limpet that inhabits *Thalassia* rhizomes in the Cayman Trench. WOLFF (1979, 1980) who examined the Soviet R/V Akademik Kurchatov material that formed the basis for MOSKALEV's description, observed that the limpets not only occupy burrows in the rhizomes created by boring bivalves, but that they may also occur in their own feeding cavities within the pithy center of the rhizome.

The bathyphytophilid shell has a cocculinacean appearance, minute and with a posterior-directed apex, but the radula is distinct from all other minute abyssal limpet groups. I have not been able to obtain material of the *Thalassia*-inhabiting limpets, but MOSKALEV's illustration clearly indicates that it is a rhipidoglossan radula with extreme reduction in the number of marginal teeth to 5–20. There are ambiguities in the drawings, but the most striking feature is the narrowness of the central field, where there is a single (poorly-developed?) rachidian, and the two massive (?) overlapping major lateral elements, which are at least superficially similar to the large overlapping elements of the addisoniid radula. The radula is strongly asymmetric. In addition to the type species, *Bathyphytophilus caribaeus*, MOSKALEV (1978) described *Aenigmabonus kurilokamtschaticus* from the Kurile-Kamchatka Trench, but the substrate association of the second species is not known.

←

Explanation of Figures 28 to 36

Figure 28. Detail of marginal tooth complex from radula illustrated in Figure 27. Note differentiation of five inner marginals with unusually large shafts and cusps. Bar = 20 μ m.

Figure 29. *Choristella* n. sp. LACM 77-374. Bar = 40 μ m.

Figure 30. *Neomphalus fretterae* McLean, 1981. Deep-sea Research Vessel (DSRV) Alvin Dive 733. Bar = 100 μ m.

Figure 31. Newly formed rachidian and left inner lateral teeth of *N. fretterae* from posterior end of radula. Bar = 40 μ m.

Figure 32. Worn rachidian and left inner lateral teeth of *N. fretterae* from same radula illustrated in Figure 31. Bar = 40 μ m.

Figure 33. Radula of an undescribed deep-sea hydrothermal vent limpet, illustrating a rhipidoglossan plan shared by five new vent species. DSRV Alvin Dive 982. Bar = 40 μ m.

Figure 34. Radula of an undescribed deep-sea hydrothermal vent limpet illustrating a new rhipidoglossan plan shared by four undescribed species. DSRV Alvin Dive 880. Bar = 100 μ m.

Figure 35. Radula of an undescribed hydrothermal vent limpet illustrating a new radular pattern not falling under standard classification and shared by two new species. DSRV Alvin Dive 879. Bar = 20 μ m.

Figure 36. Radula of a second specimen of the limpet illustrated in Figure 35. Note that the dentition from a comparable portion of the radula is poorly developed, with cusps lacking on the rachidian and laterals. DSRV Alvin Dive 879. Bar = 20 μ m.

Cocculinellid Limpets and Choristellids (Figure 29)

THIELE (1909) proposed the genus *Cocculinella* for a minute, deep-sea limpet with a unique non-rhipidoglossan radular pattern in which the rachidian is unusually small and narrow, with five heavier teeth on either side. THIELE's drawing of a half row of the radula (THIELE, 1909, pl. 1, fig. 8) and his description (pp. 21–22) indicate that the best-developed tooth is the bicuspid second lateral, and that the three outer laterals are of similar morphology but decreasing size. THIELE placed the genus with *Lepetella* in the Lepetellidae, with the interpretation that the large outer plate in the radula of *Lepetella* may be thought of as a fusion of the three outer laterals of *Cocculinella*.

Unfortunately, no subsequent collections of animals of *Cocculinella minutissima* (Smith, 1904) are available for study. However, the radula of a minute, coiled deep-sea gastropod that is commonly associated with unusual substrates shows the same basic pattern (Figure 29). These coiled gastropods have been placed in the genus *Choristella* Bush, 1897 (*Choristes auctt.*, non Carpenter, 1872). The radula has never been well understood, and there is a great deal of variation in the three drawings that have been published for the Atlantic species (VERRILL, 1882; BUSH, 1897; BOUCHET & WARÉN, 1979). The ambiguities, however, are reconciled by the scanning electron micrograph of an undescribed species (J. H. McLean, in preparation) from the Eastern Pacific (Figure 29). Ponder (unpublished) has scanned the radula of an undescribed species from off the Queensland coast, and it is comparable in numerous details (personal observation).

Although substrate data are not available in most instances, where known, choristellids occur on or in the egg cases of sharks (KURODA *et al.*, 1971) or skates (VERRILL, 1884).

The radular evidence for close affinities of a limpet and a coiled, operculate gastropod poses problems of classification that cannot be resolved within the scope of this paper and without reference to anatomy. Separate familial names are available: MOSKALEV (1971) proposed the Cocculinellidae, placing it in the Lepetelloidea, and BOUCHET & WARÉN (1979) have justified the change of the familial name Choristidae to Choristellidae. KURODA *et al.* (1971) proposed the Choristiacea (=Choristelliacea) as a superfamily, making this name available for hierarchically relating these two families of disparate shell morphology.

Hydrothermal Vent Limpets (Figures 30–36)

The remaining four groups of deep-sea limpets are all associated with unconventional substrates and food sources at abyssal hydrothermal vents that have developed at divergent oceanic plate boundaries. The animals themselves occur on basalt surfaces, on polymetallic sulfide mounds and chimneys, or on the surfaces of sessile vent organisms such as the giant vestimentiferan worms or mussels. Chemosynthetic bacteria, which are the only known primary

producers in the deep sea, form the base of the unique food chain in this environment (JANNASCH & WIRSEN, 1979, 1981; RAU & HEDGES, 1979; KARL *et al.*, 1980; CAVANAUGH *et al.*, 1981; RAU, 1981). They are consumed directly by many of the vent organisms, which may either scrape bacterial films from hard substrata or filter bacteria that are suspended abundantly in the water column. Of the extraordinary diversity of limpets that have been recovered to date from vent communities, only one species, *Neomphalus fretterae*, has been described (MCLEAN, 1981).

Nine additional limpets remain to be described (McLean, in progress) as well as a secondarily flattened operculate species that is closely related to one of the limpet groups. McLean (written communication, 1982) tentatively recognizes three new families among the remaining 10 species. I have prepared and examined radulae of all the species and find three corresponding new radula types. Scanning electron micrographs are presented for each of the major radula patterns to facilitate comparison with patterns in deep-sea limpets from other environmental settings. Detailed descriptions of these radulae will be published as an adjunct to the descriptions of the new taxa (Hickman, in preparation).

Neomphalid limpets: One of the most abundant limpets at hydrothermal vents, particularly along the Galápagos Fracture Zone, is *Neomphalus fretterae*, a gastropod of such distinctive anatomy and shell morphology as to require separate familial and superfamilial status (MCLEAN, 1981; FRETTER *et al.*, 1981). As illustrated in Figure 30, it is rhipidoglossan in form, and the most remarkable feature is the robust development of the dentition, with no indication of degeneration of teeth in the central field. The rachidian and five laterals are not only supplied with prominent pointed cusps, but the shafts are heavily reinforced, as are the complexly interlocking bases. The robust development is all the more remarkable in view of the enlarged mantle cavity and ctenidium and accompanying modifications for suspension feeding.

Although the animals seem to be sedentary, conforming in shell growth to irregularities in the substrate at their home sites, they may derive a significant proportion of their nutrition from the bacterial films that develop on the basalt. FRETTER *et al.* (1981) note larger particles in the fecal string, suggesting a mixed feeding strategy. It is clear from comparison of micrographs of newly formed teeth and teeth from the working portion of the same radula (Figures 31, 32) that the teeth are used and sustain substantial abrasion. The marginal teeth are delicate and finely serrate, frequently showing complex patterns of incomplete separation of teeth during ontogeny and irregularities that suggest lack of strong selection for normal development (HICKMAN, 1980, p. 292, fig. 6c).

Hydrothermal vent Group-A limpets: Five hydrothermal vent gastropods share the rhipidoglossan radular pattern illustrated in Figure 33. The shell morphology within this group is diverse and ranges from a minute, conispirally

coiled, operculate species (Hickman, MS) to flattened forms that properly may be called limpets. The animals have numerous features indicating that their closest relatives are trochacean gastropods. I have tentatively placed the coiled species in the Trochacea, although anatomical evidence may lend support to establishment of a separate superfamily within the suborder Trochina. Vera Fretter is currently studying the anatomy of the limpet members of this group.

In spite of the broad range of shell form, the radula is remarkably constant in morphology throughout the group. It is similar to the trochacean radular plan in the small base number of well-developed teeth in the central field and in the pattern of shaft reinforcement and within-row basal interlock. It is a relatively narrow radula, in part because the marginal tooth rows, although long, are set at a very low angle to the longitudinal axis of the ribbon. One of the most striking features of the radula is the wide spacing between rows in the central field, with tooth bases completely exposed. The wide spacing is correlated with an alternation in the position of the ends of lateral tooth rows and the beginnings of marginal tooth rows. A similar kind of accommodational alternation occurs in the neritacean radula (HICKMAN, in press).

The substrate preferences and food sources of members of this group are not well understood. Three of the five species occur at high-temperature vents on the East Pacific Rise, where they have been removed from polymetallic sulfide build-ups surrounding the high-temperature effluents. At these high-temperature vents, where water may be emitted at temperatures in excess of 350°C (in contrast to some of the "warm" vents in the Galápagos that do not exceed 22°C), there are many fewer animals. Members of this limpet group also have been recovered from washings of the giant tube worm *Riftia*, and there may be significant microhabitat specialization within the complex.

Hydrothermal vent Group-B limpets: Four limpet species share the basic radular pattern illustrated in Figure 34. These species also share a combination of anatomical features that is unique to the Gastropoda (McLean, written communications, 1982–1983). Fretter is currently studying the anatomy of these limpets as well. The radula is rhipidoglossan, and as in the other rhipidoglossan vent limpet groups, the rachidian and lateral teeth are very well developed. The rachidian is a relatively small element with a sturdy basal support for the sharply pointed and finely denticulate cusp. The most unusual element in the radula is the inner lateral tooth with its massive, complexly divided, and finely denticulate compound cusp and broadened shaft. The cusp is oriented on a strong diagonal to the longitudinal axis of the radula, connecting the rachidian cusp with the four outer lateral cusps that are situated considerably anterior to the rachidian. This arrangement produces a strong, posteriorly directed dip in the cusp row. The shafts of the four outer laterals all have

a characteristic sharp bend at mid height that accommodates the cusps of the next row posterior. Shafts also have lateral expansions to facilitate within-row interlock. The marginal teeth are numerous, with flattened shafts and finely denticulate cusps.

Hydrothermal vent Group-C limpets: Two of the limpet species collected to date from deep-sea hydrothermal vents have the non-rhipidoglossan radular plan illustrated in Figure 36. Like the radulae of bathysciadiids, addisoniids, and lepetellids, it does not fit into the standard classification of radula types. The bases, shafts, and cusps of the five radular elements are unique in form. The single most unusual feature of the radula is the interaction between the base of the second lateral and the cusp of the third lateral of the same row. Within-row interactions in other radulae are cusp-cusp or base-base, but in this group there is a prominent basal projection or fold on the second lateral that fits or locks beneath the cusp of the adjacent third lateral.

The rachidian is a small tooth with a pointed triangular cusp. Its base is a short transverse bar that fits into deep pockets on the bases of the inner lateral teeth. The three inner laterals are of similar general form with thin, relatively broad and flexuous cusps, complex sinuous shafts, and interlocking basal folds. The outer lateral is a broad, flattened, spoon-shaped element with a semicircular rim of folded-over or enrolled chitin that is perhaps best not termed a cusp.

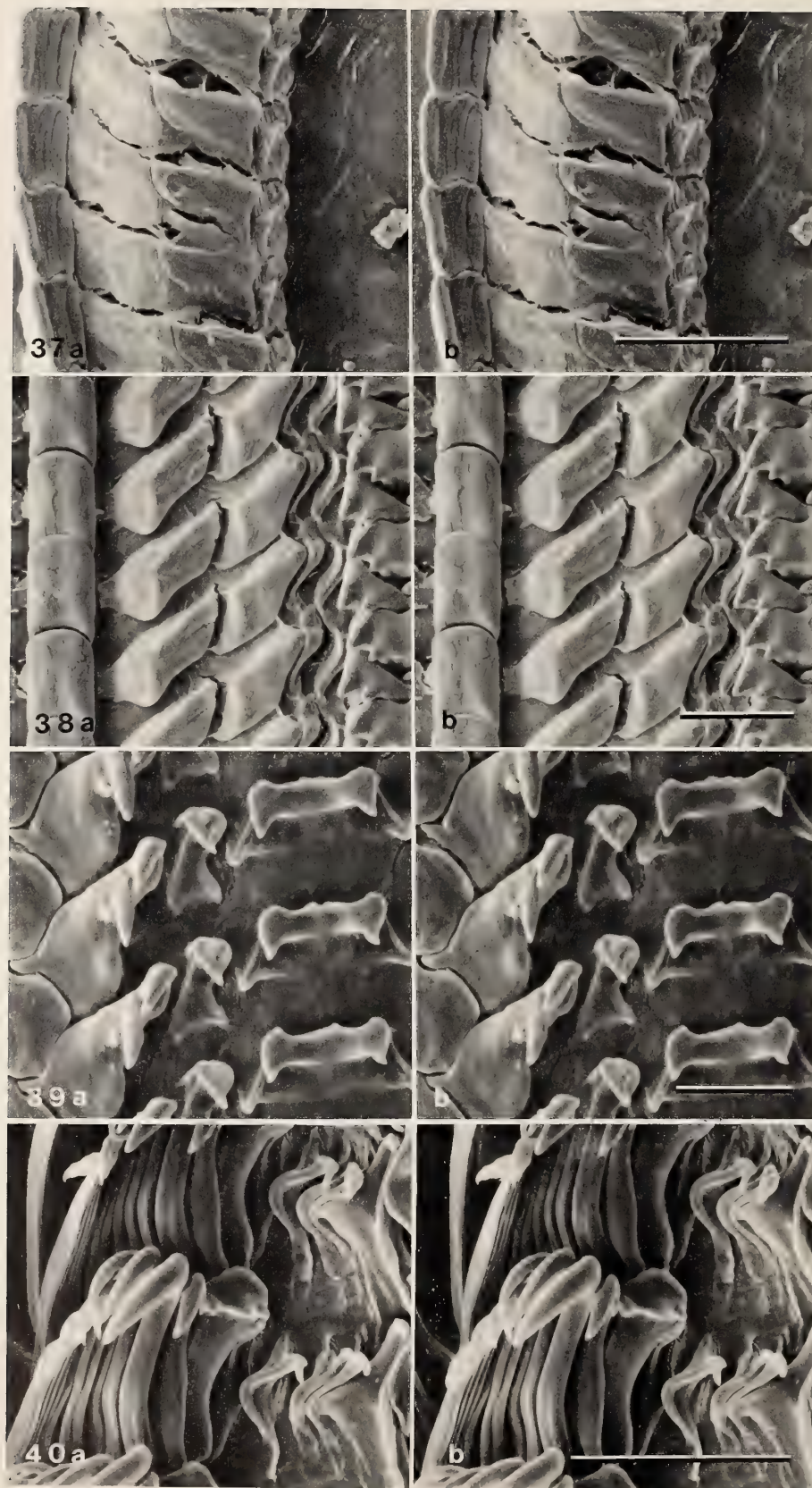
The entire radula is very small and insubstantial, and in one specimen that I have prepared (Figure 36) failure of normal cusps to develop suggests that selection pressure to reproduce faithfully the standard plan is not great.

DISCUSSION

Radular Characters and Systematics

Sixteen distinct deep-sea radular patterns are illustrated in this paper. Although two of them are docoglossan and nine are rhipidoglossan, five do not fit the standard classification scheme. Even the docoglossan and rhipidoglossan radulae have patterns that are distinct in many details from those of related shallow-water groups, and in some cases deep-water families cannot be related to extant shallow-water families or to one another on radular characters. Some discussion of the role of radular characters in further systematic evaluation of deep-sea limpets is in order.

Although a primary purpose of this paper is to provide data for dealing with the systematics and classification of deep-sea limpets, the radular data are biased toward an emphasis of differences rather than similarities. Radular characters will continue to be important in dealing with these taxa, but they will be most valuable in differentiating genera and species within families. The major patterns are too distinct from one another and from patterns



in other gastropod groups to provide reliable data for establishing higher relationships.

This leaves us with something of a dilemma as to where to seek shared characters that will enable us to place many of these taxa into phylogenetic perspective. The shells are extraordinarily similar, but in shell form we are dealing with strong evolutionary convergence. Shell microstructure may prove useful, although the emphasis should be on details of the mineral species and fabrics that are present rather than on absences that may be due to a secondary simplification of structure. Loss of shell layers, particularly the inner nacreous layer, appears to be strongly correlated with small size (Hickman, MS), and therefore should not be heavily weighted in taxonomy. The most reliable clues should be revealed through detailed comparative anatomical studies. Here too, however, it must be remembered that the limpet grade of evolution requires modifications of anatomical blueprints that were accommodated to life in a coiled shell. Detailed comparative histological analyses are a formidable task, but will probably be necessary because gross anatomical features are inadequate to establish relationships.

Ecological and Evolutionary Implications

What we now know about the radular morphology, habitats, and substrates of deep-sea limpets has some important evolutionary and ecological implications. It has long been held that feeding structures in organisms are easily modified in relationship to substrates and food preferences and, thus, are not likely to provide good characters for differentiating taxa (see HOUBRICK, 1978, and references therein). Although this may be the case in some groups of gastropods, it is not a generalization that can be extended to the entire class (HICKMAN, 1980, 1982). This is nowhere better demonstrated than in the taxa of deep-sea limpets that have converged on feeding on unconventional substrates. For example, cocculinid limpets recovered from wood have the same radular pattern as the cocculinid limpet recovered from squid beaks. Bathysciadiid limpets from squid beaks have a radular pattern that shows no convergence with the cocculinid squid-beak species. Likewise, wood-ingesting docoglossans, wood-ingesting cocculinids, and wood-ingesting pseudococculinids retain highly distinctive dentition patterns. In each of these three groups, there are formidable, major food-preparing

teeth that we may infer to be *adequate* designs for dealing with water-logged wood. However, it would be difficult to argue that any one of these solutions is an optimal one.

Many evolutionary biologists and ecologists have based their research on the assumption that evolution involves a great deal of fine-tuning and optimization; but ideal solutions may be prohibitively costly to produce and maintain, and many organisms may be built simply to "get by" (COWEN, 1981; HICKMAN, 1982). Limpets in the deep sea seem to have developed a number of alternative solutions to feeding on a number of difficult or unusual substrates.

What is peculiar is the strong convergence in shell shape. It is not at all clear what the advantages of secondary flattening are to so many forms that colonize unconventional substrates in the deep sea. It is certain that the limpet shell form does not have the same protective functions in small deep-sea limpets that it does in shallow-water limpets.

Connections Between Cambrian Limpets and Deep-Sea Limpets

This brings us again to the question of size and the proposition in the introduction that there may be some connection between the predominance of small cap-shaped shells in the early evolution of the Mollusca and the plethora of such forms in the deep sea today. If we accept the proposition that the protective mechanical functions of shell form that work in large shallow-water limpets do not apply to minute deep-sea limpets or to the Cambrian early mollusk radiations, what similarities do these forms share that might suggest alternative hypotheses?

Although VERMEIJ (1971, 1973) has correctly emphasized the increase in the morphological diversity of gastropod *shells* as a result of increase in the number of parameters controlling shell geometry, it does not follow that more complex shell geometry permits greater diversity of anatomical organization. The simple geometric form of the limpet permits an extraordinary variation in anatomical organization.

Lindberg and Wright (in MS) have shown that shell shape can place interesting volumetric constraints on the ways that anatomical plans can be varied with respect to reproductive modes and that some modes are more likely in limpets. Another important constraint, I believe, is that on respiration. The uncoiled limpet shape, especially when

←

Explanation of Figures 37 to 40

Paired stereo micrographs illustrating topographic differences in four deep-sea limpet radular groundplans.

Figure 37. *Bathysciadium pacificum* (same radula illustrated in Figure 9). Bar = 50 μ m.

Figure 38. *Addisonia* n. sp. LACM, uncataloged. Bar = 50 μ m.

Figure 39. *Lepetella tubicola* (radula illustrated in Figure 11). Bar = 20 μ m.

Figure 40. *Pseudococculina* sp. C (radula illustrated in Figure 27). Bar = 40 μ m.

coupled with small size, provides a great deal of versatility in modes of respiration. Discrete respiratory organs are not essential in small flat animals. And even when present, such organs do not require active control of water currents. Although much has been made of the position of the "mantle cavity" in the interpretation and classification of early mollusks, the concept of the *cavity* needs critical reexamination.

The concept derives in part from the standard drawings and discussions of the Hypothetical Ancestral Mollusk (YONGE & THOMPSON, 1976). A number of authors have advised of the dangers in using HAM to understand molluscan evolution (e.g., MORTON, 1967; STASEK, 1972; POJETA, 1980), but many of the implications of the concept have been perpetuated by its harshest critics. A mantle cavity need not be present at all. In flat, uncoiled monoplacophoran limpets the respiratory structures are situated in a pair of pallial grooves, not in a cavity. The notion that the development of a dorsal calcified covering created a mantle cavity is an oversimplification, and the conclusion that it *necessitated* the development of gills (POJETA, 1980) is unwarranted.

The development of a distinct mantle cavity as opposed to grooves, and increasingly efficient gill structures and methods of passing water currents over them, are major themes in gastropod evolution and have undoubtedly permitted them to become large and active animals.

It is significant to note, however, that, in animals with the limpet form, we can find everything from no discrete respiratory organs at all to animals with true molluscan ctenidia. And, in between, we can find animals with both ctenidia and secondary gills and animals with secondary gills but no ctenidia. We also see a range in the numbers of these structures and the way that they are housed. Modern limpets are much more adventuresome with respiration than are coiled gastropods, and there is some good reason to believe that experimentation with respiration was important in Cambrian mollusks. This is suggested, for example, by the development of tubular structures (RUNNEGAR & POJETA, 1974; RUNNEGAR & JELL, 1976) in a number of tall cone-shaped, but minute, Cambrian shells.

It must be remembered that modern deep-sea limpets are not living fossil holdovers from the Cambrian. There is too much evidence for secondary derivation from coiled ancestors. But, keeping this fact in mind, the living minute deep-sea limpets provide a wealth of anatomical information about the possibilities for organization and experimentation in the context of limpet geometry on a small scale.

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NOTE ADDED IN PROOF

A paper has just appeared in which B. A. MARSHALL (1983. The family Cocculinellidae (Mollusca: Gastropoda) in New Zealand. Nat. Mus. New Zealand, Records 2(12):139–143) provides new evidence on the biology and morphology of *Cocculinella*. It fails to support the relationship with the Choristellidae proposed herein. The

radula of a new shallow-water (13 m) New Zealand species is of a plan distinct from all the patterns illustrated in this paper, and the specimens were removed from fish bone. Marshall also reexamined syntypes of the type species and discovered that they were on fish bone, not on 'waterlogged wood' as stated in the original description.

Additions to the Opisthobranch Mollusk Fauna of Marin County, California, with Notes on the Biology of Certain Species

by

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Abstract. Seven species of opisthobranch Mollusca from Marin County, California are discussed, and certain aspects of their biology presented. Three species are new additions to the faunistic list of this area; one sighting represents a geographical range extension.

THE OPISTHOBRANCH mollusks of Marin County, California have been extensively documented in numerous reports (STEINBERG, 1960, 1963; MARCUS, 1961, 1964; GOSLINER, 1968; GOSLINER & WILLIAMS, 1970, 1973; WILLIAMS, 1971; GODDARD, 1973; BEHRENS, 1980b; JAECKLE, 1981) in which a total of 74 species have been reported. Since 1977, this aspect of the littoral invertebrate fauna has been intermittently examined, and several species, previously unreported from this area, have been observed. These observations, as well as aspects of the biology of certain species found in Marin County are reported here. Species not previously reported from Marin County are denoted by an *; extension of the geographical range is denoted by a **.

Systematic List of Discussed Species

Subclass Opisthobranchia

Order Nudibranchia

Suborder Doridacea

Family Cadlinidae

Cadlina sparsa (Odhner, 1921)**

Family Aldisidae

Aldisa sanguinea (Cooper, 1863)*

Suborder Dendronotacea

Family Dotidae

Doto kya Marcus, 1961

Suborder Arminacea

Family Janolidae

Janolus barbarensis (Cooper, 1863)*

Janolus fuscus O'Donoghue, 1924

Suborder Aeolidacea

Family Flabellinidae

Flabellina trilineata (O'Donoghue, 1921)

Family Tergipedidae

Tenellia adspersa (Nordmann, 1845)*

Cadlina sparsa (Odhner, 1921)

Two specimens of this eudoridoidean species were collected in a rocky, semi-protected littoral locality, the Frontier Arts Nature Reserve (latitude 37°52'22"N; longitude 122°36'56"W). These collections represent a geographical range extension, as well as an addition to the opisthobranch fauna of Marin County. The previous northernmost occurrence of *Cadlina sparsa* was Monterey Bay, Monterey County, California (BEHRENS, 1980a). The coloration of these specimens differed from previously published accounts. Typically, the rhinophores are light yellow to yellowish-brown in coloration (McDONALD, 1977); however, the rhinophoral coloration of the collected specimens was light brown with numerous black spots on the rhinophoral lamellae. A voucher specimen has been deposited in the invertebrate collection of the California Academy of Sciences bearing the voucher number CASIBP 030954.

Aldisa sanguinea (Cooper, 1863)

Although the geographical range of *Aldisa sanguinea* extends from Coos Bay, Oregon to San Diego, California and in the Gulf of California, Mexico (BERTSCH &

JOHNSON, 1982), this species has not been reported from Marin County. This species has been sighted in two rocky littoral areas, Muir Beach Overlook (latitude 37°52'21"N; longitude 122°36'56"W) and the Frontier Arts Nature Reserve.

Doto kya Marcus, 1961

This dendronotacean species is common in rocky littoral and estuarine habitats of Marin County. Despite the abundance of *Doto kya* in central California, the biology of this species is poorly known. In rocky littoral habitats of Marin County, specimens of *D. kya* have been observed preying upon the leptomedusan hydrozoan *Obelia dichotoma* (Linnaeus, 1758) and the anthomedusan species *Sarsia* sp. *Doto kya*, in estuarine areas of San Francisco Bay, feeds on *O. dichotoma*. The spawn masses of *D. kya*, deposited on the hydrocauli of *O. dichotoma* colonies, have been found in both habitats.

Janolus barbarens (Cooper, 1863)*

Janolus fuscus O'Donoghue, 1924

GOSLINER (1981, 1982) synonymized the genus *Antiope* Hoyle, 1902, with *Janolus* Bergh, 1884, and reinstated *J. fuscus* as a distinct species. *Janolus barbarens* and *J. fuscus* have been viewed as a single species for 15 years (GOSLINER, 1982) and, as a result, the geographical ranges of both species have been combined by most authors. GOSLINER (1982) mentioned this range overlap but did not indicate their limits. In Marin County, *J. barbarens* has been found on wharf pilings at Sausalito, San Francisco Bay (latitude 37°47'N; longitude 122°21'W) and *J. fuscus* has been collected at Muir Beach Overlook and the Frontier Arts Nature Reserve.

Flabellina trilineata (O'Donoghue, 1921)

GOSLINER & GRIFFITHS (1981) synonymized the genus *Coryphella* Gray, 1850, with *Flabellina* Voigt, 1834, due to a lack of genus-specific morphological characters. In Marin County, *Flabellina trilineata* occurs in both estuarine and marine habitats. At the Muir Beach Overlook study site, this species was observed feeding on the anthomedusan hydroid species *Tubularia marina* (Torrey, 1902) and *Sarsia* sp. The specimens of *F. trilineata* selectively preyed upon the tentacles of *T. marina*, leaving the remaining portion of the polyp intact. This feeding selectivity differs from COOPER's (1980) report that *F. trilineata* consumes the entire polyp of *Tubularia crocea* (Agassiz, 1862) in Elkhorn Slough, Monterey County, California.

Tenellia adspersa (Nordmann, 1845)*

Large numbers of *Tenellia adspersa* have been observed on wharf pilings in Sausalito, San Francisco Bay, feeding on *Obelia dichotoma* during May–August, 1982. Although *T. adspersa* has been previously reported from San Fran-

cisco Bay (STEINBERG, 1960, 1963; BEHRENS, 1980b), this is the first reported sighting from Marin County. The examined specimens were small (<5 mm in length) and exhibited a wide variation in the amount of black pigment spots present on the dorsal surface. Eastern Pacific specimens typically possess a light cream body coloration with "a few" black pigment spots on the dorsum (McDONALD, 1977). BROWN (1980), however, reports that British specimens of *T. adspersa* exhibit a variable density in black "speckling." In several specimens collected in Marin County, the black spots were so dense that the dorsum appeared black. Along with these darkly pigmented individuals were collected specimens that exhibited the typical coloration pattern. The radula of a darkly pigmented specimen agrees with the radula of *T. adspersa* as depicted in BROWN (1980).

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Specialized Feeding in Mitrid Gastropods: Evidence from a Temperate Species, *Mitra idae* Melvill

by

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Abstract. The neogastropod *Mitra idae* Melvill is the only member of the family Mitridae on the California coast. Although suspected of being a specialized predator, its food preferences have never been quantified. This study documents the feeding of *M. idae* on sipunculans. Laboratory experiments and gut analysis of field-collected specimens of *M. idae* have revealed that it is a specialized predator preferring the sipunculan *Phascolosoma agassizii* Keferstein.

INTRODUCTION

MEMBERS OF THE gastropod family Mitridae are most common in tropical waters, but some are present in temperate marine waters (CERNOHORSKY, 1970; ABBOTT, 1974; MCLEAN, 1978; KAY, 1979). Although PONDER (1972) has given detailed descriptions of the digestive tract, little is known about the diet. The few species investigated have been shown to prey on sipunculans (KOHN, 1970, 1978; WEST, 1979). Quantitative dietary information is available for only two members of the family, *Mitra literata* Lamarck, of intertidal beaches in Hawaii, where it specializes on the sipunculan worms, *Phascolosoma* spp. and *Aspidosiphon elegans* Chamisso and Eysenhardt (KOHN, 1970), and *Mitra flavocingulata* of Easter Island, which KOHN (1978) has reported feeding on a species of *Phascolosoma*. TAYLOR (1975) has found juveniles of *Mitra assimilis* in Hawaii to feed on small mollusks under laboratory conditions.

There is some uncertainty as to the number of *Mitra* species occurring along the central California coast. WEST (1979) reports two, *M. idae* and *M. catalinae*, which, he reports, differ in radula structure and proboscis morphology, but which are otherwise alike externally except for size, *M. catalinae* being less than 30 mm in length. However, MCLEAN (1978) considers *M. catalinae* synonymous with *M. idae*. ABBOTT (1974) questioned whether it was a dwarf form of *M. idae*, and MORRIS *et al.* (1980) mention only *M. idae*. If there are two species virtually indistinguishable externally except for size as WEST (1979) has suggested, it means that small animals (<30 mm) may

be either juvenile *M. idae* or *M. catalinae*, and would be indistinguishable without dissection. We were not aware of the potential presence of two species until this study was completed and specimens had been discarded after gut dissection; thus, we were unable to undertake radula and proboscis dissections of small specimens to attempt to verify WEST's (1979) contention. Therefore, those specimens that we have considered here as juvenile *M. idae* (<28 mm) could be a mixture of the two species if WEST's (1979) contention that there are two species is substantiated by other malacologists. In either case, this does not invalidate our main argument of dietary specialization regardless of size. We prefer, pending presentation of more evidence, to follow MCLEAN (1978) and consider all California mitrids as members of one species, *M. idae*.

Mitra idae Melvill is restricted to kelp forests and the low intertidal zone (MCLEAN, 1978; MORRIS *et al.*, 1980). Previous studies of this species have dealt with taxonomy and radular arrangement (CERNOHORSKY, 1966, 1970; COAN, 1966; CATE, 1967), functional morphology (WEST, 1979), and reproductive patterns and behavior (CATE, 1968; CHESS & ROSENTHAL, 1971; KELLOGG & LINDBERG, 1975). Although MORRIS *et al.* (1980) report *M. idae* to be a specialized carnivore, no documentation is provided, nor is the prey identified. Moreover, CATE (1968) was unsuccessful in feeding a variety of potential prey items to *M. idae* in laboratory aquaria. She did not report whether sipunculans were offered to the *M. idae*. WEST (1979), however, has observed *M. idae* to feed upon the sipunculan *Phascolosoma agassizii* and the vermetid gastropod *Petalconchus montereyensis* in the laboratory. His

accounts represent the most complete descriptions of feeding in the species.

The present study further quantifies the diet of free-living *Mitra idae* and establishes preferences in laboratory experiments. This information should help to establish the role of predation by *M. idae* in the kelp forest and the more general occurrence of sipunculan feeding within the family. Other species and genera remain to be studied to establish a general pattern of specialized feeding on sipunculan worms.

METHODS

The main study area was the kelp forest off Point Cabrillo, Pacific Grove, California (36°37'N; 121°53'W). Additional collection of *Mitra idae* for gut content analyses was done off Del Monte Beach, Pacific Grove (36°37'N; 121°53'W), and Stillwater Cove (36°33'N; 121°56'W) (Figure 1). Descriptions of these kelp forests are given in LOWRY & PEARSE (1973) for Point Cabrillo, in BURNETT (1972) and HOFFMAN (1981) for Del Monte Beach, and in FOSTER (1982) for Stillwater Cove.

All sampling and collecting were done with SCUBA. Estimates of abundance of *M. idae* were made at Point Cabrillo in April and May, 1981. Water depth varied from 5 to 10 m. Random samples were taken along 25-m transects within a 0.25-m² quadrat. All *M. idae* found within these quadrats were counted and measured. Animals used for gut-content analyses were collected haphazardly during day and night, and were boiled shortly after collection to stop further digestion. After recording wet weight and measuring length from the apex of the shell to tip of siphonal canal, each shell was cracked open and the digestive tract dissected. Prey were identified and counted, and state of digestion noted.

Laboratory feeding experiments were conducted to document prey preferences employing two species of sipunculans and other potential prey, and to observe feeding behavior. One sipunculan species, *Phascolosoma agassizii*, was collected from local rocky intertidal areas and the holdfasts of drift kelp. The other sipunculan, *Themiste pyroides* (Chamberlain), was collected from subtidal shale. Prey wet weights were recorded before and after feeding experiments. One set of experiments evaluated the preference of *M. idae* for the two species of sipunculans. In each experiment, one *M. idae* was placed in a dish with one *P. agassizii* and one *T. pyroides*. The experiment was repeated 2–4 times for each *M. idae* used. The dishes were covered with a fine screen to prevent escape and were held in laboratory aquaria with running sea water. Observations continued until one of the prey was consumed or attacked. Sipunculans of similar size were used when possible; however, individuals of *T. pyroides* were generally larger than *P. agassizii*.

In a second set of experiments, each species of prey was presented separately to a specimen of *M. idae*. In addition to the two species of sipunculans, *M. idae* was also pre-

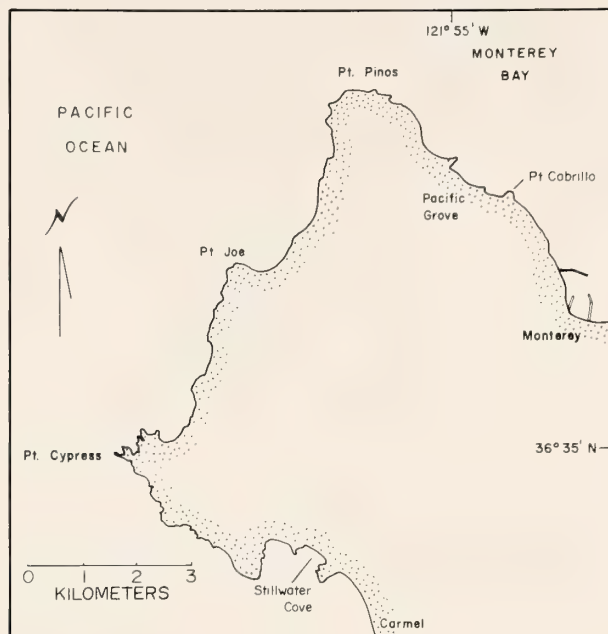


Figure 1

Location of study areas in central California.

sented with the echiuroid worm *Urechis caupo* Fisher and MacGinitie, and the holothuroids *Eupentacta quinquesemita* (Selenka) and *Cucumaria pseudocurata* Deichmann. *Urechis caupo* is a close taxonomic relative of the sipunculans, and the two holothuroids are similar in size and shape to sipunculans.

RESULTS

Individuals of *Mitra idae* were observed subtidally on rock walls, in crevices, in sand pockets, on old holdfasts of the kelp *Macrocystis pyrifera*, under the cover of red algae (*Gigartina* spp. and *Rhodomenia* spp.) and in tube beds of the polychaete *Diopatra ornata* Moore. Although the abundance of *M. idae* was only 0.81/m² (SD = 0.54; n = 106) at Point Cabrillo, individuals were seen in aggregations of up to five individuals. KOHN (1970, 1978) observed 0.05–0.22 *Mitra litterata*/m² in Hawaii and 0.12 *M. flavocingulata*/m² at Easter Island.

Size-frequency plots revealed two distinct size classes at Point Cabrillo, one near 15–20 mm and the other near 40 mm (Figure 2). CHESSE & ROSENTHAL (1971) found mean shell lengths for copulating *M. idae* in southern California at 35 mm for males and 51 mm for females. Therefore, the smaller size group (<28 mm) probably was composed mostly of juveniles or a mixture of juveniles and *M. catalinae*.

The gut contents of 41 *M. idae* were examined (Table 1). Three of these individuals were collected at Stillwater Cove, six from Del Monte Beach, and the remaining an-

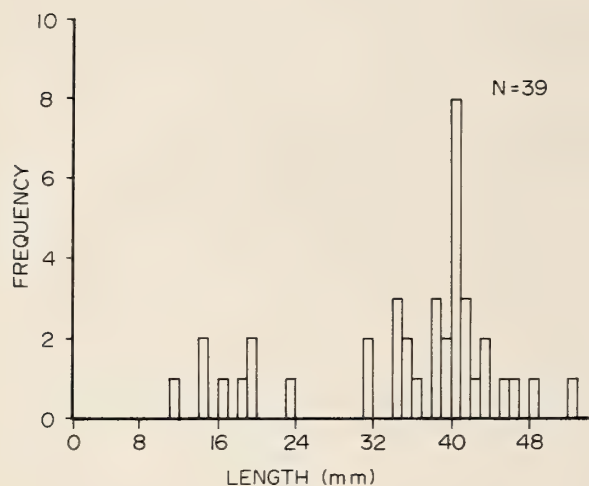


Figure 2

Length-frequency histograms for *Mitra idae* collected at Point Cabrillo. Note the separation of a large ("adult") and small ("juvenile") size class.

imals from Point Cabrillo. Food was found in 22 guts (54%). Sixteen guts contained whole sipunculans or fragments. Five had unidentifiable organic matter, and one gut had the remains of what appeared to be a nemertean worm. The sipunculan was identified as *Phascolosoma agassizii* in 13 of the 16 guts. Only five *M. idae* were collected at night. These were all collected at Point Cabrillo. Two of these individuals had empty guts, two contained fragments of *P. agassizii*, and one had fragments of a nemertean. Most of the 16 juvenile *M. idae* had empty guts; however, one contained part of a *P. agassizii*, and

Table 2

Choice of prey when *Mitra idae* was offered both sipunculans, *Phascolosoma agassizii* and *Themiste pyroides*. *Phascolosoma agassizii* was preferred in every experiment.

	Number of trials	Prey consumed	
Mitra #1	5	<i>Phascolosoma</i> (5)	<i>Themiste</i> (0)
Mitra #2	6	<i>Phascolosoma</i> (4)	<i>Themiste</i> (0)
Mitra #3	3	<i>Phascolosoma</i> (1) *	<i>Themiste</i> (0)
	14	10	0

* *Phascolosoma* attacked but later released (see text).

five others contained unidentifiable organic matter. Among the 25 adults, two contained whole specimens of *P. agassizii* (<0.1 g), and 10 had parts of this species. The sipunculan prey in three adult guts could not be identified to species.

The two-choice feeding experiments indicated that *Mitra idae* has a strong preference for one of the two sipunculan species. *Phascolosoma agassizii* was attacked in 10 of 14 trials. *Themiste pyroides* was not attacked (Table 2). Feeding experiments containing one species of potential prey showed the same pattern. *Phascolosoma agassizii* was consumed in 30 of 45 trials (67%). *Themiste pyroides* was not consumed in any of five exposures to *M. idae* (Table 3). Fewer trials were made with *T. pyroides* because of the longer duration of each experiment. In one experiment, a specimen of *M. idae* was starved for 17 days prior to exposure to a *T. pyroides*. The *T. pyroides* was attacked and held by the proboscis of *M. idae* for over six hours before it was released. However, the *M. idae* did not consume the *T. pyroides*, which suffered no apparent damage

Table 1

Gut contents of *Mitra idae* collected at three areas in central California and in "adult" and "juvenile" sizes from all areas.

Area	Number of guts examined	Number empty	Number with sipunculans	Amorphous organic matter	Other*
Stillwater Cove	3	0	0	3	0
Del Monte Beach	6	1	5	0	0
Point Cabrillo	32	18	11	2	1
	41	19	16	5	1
Size of <i>Mitra idae</i>					
"Juveniles" <28 mm	16	10	1	5	0
"Adults" ≥28 mm	25	9	15	0	1
	41	19	16	5	1

* Fragment of nemertean worm.

Table 3

Feeding experiments offering *Mitra idae* either one or the other of the sipunculan, *Phascolosoma agassizii* or *Themiste pyroides*. Only *P. agassizii* was consumed.

Prey species	Number of trials	Total number consumed	Number eaten whole	Pierced and eaten	Attacked, not eaten
<i>Phascolosoma</i>	45	30	25	5	1
<i>Themiste</i>	5	0	0	0	1

from the attack, and it remained alive in a holding tank. *Mitra idae* neither attacked nor consumed the three sipunculan-like prey, *Urechis caupo*, *Eupentacta quinquesemita* and *Cucumaria pseudocurata*, in similar feeding experiments.

Laboratory feeding observations indicated two methods of attack and consumption of the *Phascolosoma agassizii*. Prey either were ingested whole or the integument was punctured by the radula and the internal contents removed through the hole, presumably by a mechanism described by WEST (1979). Considering all experiments, 81.5% of the *P. agassizii* were consumed whole ($n = 40$). Prey weighing less than 0.3 g were always ingested whole, but larger individuals (up to 0.8 g) were taken whole as well. Only seven individuals were eaten by puncturing the integument of the sipunculan. These prey were relatively large compared to those eaten whole, and ranged in size from 0.3 to 0.76 g (Figure 3). The weight loss of pierced prey averaged $64 \pm 17\%$ ($n = 7$) and all pierced animals died.

DISCUSSION

Mitra idae seems to be a specialized carnivore. Although we have tested only one other sipunculan species, gut contents and laboratory feeding experiments indicate that the sipunculan *Phascolosoma agassizii* is the dominant or preferred prey. *Phascolosoma agassizii* is the most abundant sipunculan at all three study areas on the Monterey Peninsula (HOFFMAN, 1981; personal observations). Despite the presence of another sipunculan, *Themiste pyroides*, in the field (HOFFMAN, 1981) and in feeding experiments, this species was not consumed by the gastropod (Tables 2, 3). An echiuran worm and two holothurians also were not eaten in laboratory feeding experiments. Moreover, the guts of *M. idae* collected in the field did not contain any of the abundant polychaete groups that co-occur with *M. idae* (e.g., onuphids, terebellids, sabellids, syllids).

Specialized feeding on sipunculan worms was first established by KOHN (1970, 1978) for the tropical species *Mitra litterata* and *M. flavocingulata*. Now, evidence suggests a similar situation for the temperate species *M. idae*. Although three species is a small sample of the 500 or so

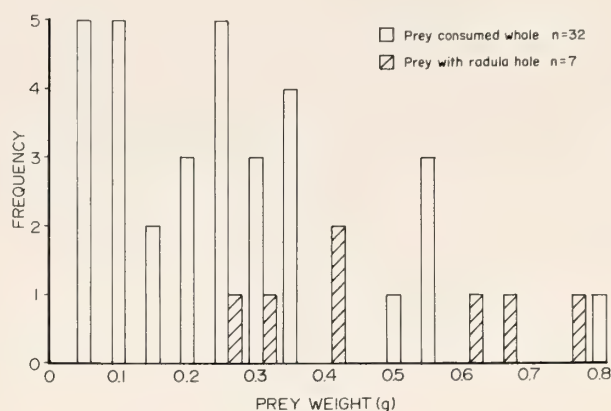


Figure 3

The relationship between the size of *Phascolosoma agassizii* and the method of prey consumption. Smaller prey were generally eaten whole and only larger individuals were eaten by puncturing the integument of the prey and inserting the proboscis.

species from this family, the geographical separation of *M. idae* from *M. litterata* and *M. flavocingulata* suggests that a general feeding pattern concentrating on sipunculans may emerge, at least for this genus. Indeed, WEST (1979) has determined that the epi-proboscis of *M. idae* functions to locate, retrieve, and hold soft-bodied prey, in particular, sipunculans. Perhaps sipunculan worms will be the dominant prey for the entire family. Present knowledge does not allow a critical evaluation of this hypothesis, but the distinct morphological similarities in the alimentary canal among members of the family Mitridae reported by PONDER (1972) would argue for this.

Laboratory feeding observations indicated two modes of prey consumption for *Mitra idae*. A few sipunculans were eaten by puncturing the integument, inserting the proboscis, and removing the body contents, as WEST (1979) has described; but most were consumed whole, especially the smaller-sized prey. The proboscis of mitrids may be extended the length of the shell (WILSON & GILLET, 1972; personal observations). The ability to extend the proboscis a long distance is of practical importance in feeding upon prey that lodge deep in crevices, holdfasts, or other substrata. The two modes of consuming prey also may be of significance in that the extraction of a strongly wedged sipunculan is not necessary. The frequency of puncture feeding is difficult to assess in the field, as empty guts can indicate either the absence of prey or faster digestion of the internal contents of a pierced prey compared to the outer integument of an animal consumed whole.

Gut contents and laboratory experiments suggest that the feeding habits of *Mitra idae* may be more closely related to behavioral preferences and not to prey availability. The ability to survive without food for at least 8–12 months (CATE, 1968; personal observations) supports the

idea that prey availability may not be of critical importance. Size selective predation also may be feasible. Evidence from the few whole sipunculans found in gut contents of *M. idae*, as well as laboratory observations, seem to support this idea. Perhaps future studies will reveal important similarities in the foraging tactics of mitrid gastropods that will allow generalizations to be made about the family. Specialized feeding on sipunculan worms by tropical and a temperate *Mitra* suggests that similar evolutionary processes affected the development of these predator-prey interactions.

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Homing in the West Indian Chiton *Acanthopleura granulata* Gmelin, 1791

by

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Abstract. The homing behavior of the chiton *Acanthopleura granulata* was studied on high-, moderate-, and low-energy rocky shores in the Bahamas. Chitons on low-energy shores tended to home more frequently than chitons on higher-energy shores. Chitons on higher-energy shores tended to make more frequent nighttime excursions from their home and to travel greater distances than chitons on low-energy shores, possibly because lower food availability on higher-energy shores may force the chitons to increase their grazing effort.

INTRODUCTION

HOMING IS A very common phenomenon in some groups of mollusks. It has been described in several species of gastropods (McFARLANE, 1981; WELLS, 1980; COOK, 1979; COLLINS, 1977; MACKEY & UNDERWOOD, 1977; and others) and chitons (GLYNN, 1970; THORNE, 1968). *Acanthopleura granulata* Gmelin, 1791, a West Indian chiton, is very common on the intertidal limestone shores in the Bahamas. Individuals generally remain stationary on their rock substratum during the daylight hours and forage for endolithic and surficial algal food at night (GLYNN, 1970). Unlike that of some other species of chitons, the foraging of *A. granulata* does not seem to be influenced by tidal height (NEWELL, 1979). Upon completion of its foraging activity, *A. granulata* often returns (homes) to its original site of attachment. Because individuals do not always come to rest exactly on their old site of attachment and often orient themselves differently (GLYNN, 1970), the term "homing" as used in this study is not being used in the strictest sense (COLLINS, 1977). In this study, I describe the differences in homing behavior of individual *Acanthopleura granulata* inhabiting high-, moderate-, and low-wave energy shorelines in the Bahamas.

MATERIALS AND METHODS

In order to compare homing activity of *Acanthopleura granulata* on high-, moderate-, and low-energy shorelines, observations were made on various rocky limestone (Karrenfeld) (GARY *et al.*, 1974) shorelines in the Bahama Island chain (Figure 1). High-energy zones (Stations 1, 4, 6, 7) were on shorelines exposed to the open ocean and

were generally subjected to surf of one to several meters in height. These shorelines were usually wetted by spray and wave swash for a large part of the day. Moderate-energy shorelines (Stations 5, 8) were exposed to some waves and spray at high tides and during windy weather. Low-energy shorelines (Stations 2, 3) were exposed to little or no wave or spray activity and were wetted only at flood tides when water covered the substrate.

Individual *Acanthopleura granulata* and their attachment sites (=homes) were marked with nail polish. The following day, the marked homes were checked to determine whether the chitons were present or absent from where they were marked the previous day. If the chiton was absent from the home it occupied the previous day, the animal was located (if possible) and its new site of attachment (home) was marked. The distance between the original and new home was measured. If the animal could not be located, it was counted as absent. Observations were made from two (Indian Cay) to six (San Salvador) consecutive days.

Because many chitons (especially in low- and moderate-energy zones) were generally at their original home when observed each day, observations also were made on nights when low tides occurred to determine whether those animals were foraging at night and returning to their homes or simply were not leaving their homes at all. The distances between the foraging chitons and their homes were measured. Personal safety considerations prevented nighttime observations on high-energy shores.

A Student's *t* test was used to compare distances traveled between chitons (*Acanthopleura granulata*) in low-energy areas and chitons in moderate-energy areas. Be-



Figure 1

Localities where observations were made. 1: Indian Cay, near West End, Grand Bahama Island. 2, 3, 4: Black Rock, near Moors Island, Abaco Chain. 5, 6: North Point, San Salvador Island. 7, 8: Barkers Point, San Salvador Island.

cause an F_{\max} test indicated that distance data were not normal, all distance data were transformed using a log transformation.

Caloric values of substrata in a moderate- (Station 8) and low- (Station 2) energy zone were compared. Samples of the limestone substrate were taken by scrubbing the substrate with a wire brush and rinsing the loosened limestone and its associated endolithic and surficial algae into a jar. The samples were kept frozen until they were returned to the laboratory where they were filtered, dried, and ground into a powder. Samples were mixed with benzoic acid (50% acid, 50% sample) and their caloric value measured in a Phillipson microbomb calorimeter (PHILLIPSON, 1964).

Because the topography and density of the substratum were similar on all islands studied, caloric values are reported in calories per milligram of substratum rather than in calories per area of substratum. Irregularities in the substratum surface made it difficult to remove limestone evenly from a specific area. Twelve replicates were done for each sample. A t test was used to compare the caloric

value of samples taken from low- and moderate-energy zones.

RESULTS

From a total of 162 observations, about 43% of the *Acanthopleura granulata* had moved from the point at which they were marked the previous day. Far fewer chitons were found at the point where they were marked in high-energy zones (15%) than in moderate- (56%) or low- (93%) energy zones (Figure 2). Although only a small number of chitons observed in low-energy zones were found absent from their home the following day, nighttime observations showed that 59% of the marked chitons in low-energy zones were away from their home at night. All of these chitons had returned to their home by morning. In moderate-energy zones, about 70% of the marked chitons were observed away from their home at night, but only 56% of these chitons had returned back to their home by morning (Figure 3). Since nighttime observations could not be made in high-energy zones, it is not known whether the chitons

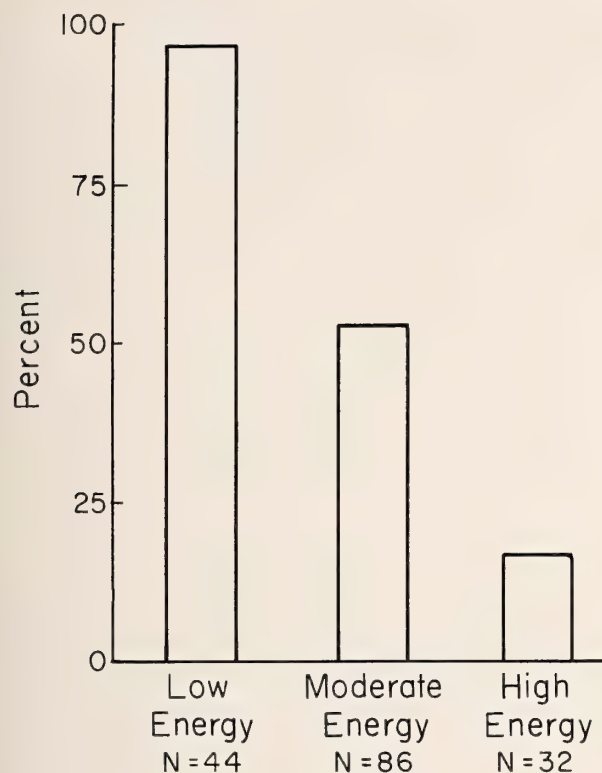


Figure 2

Percent of chitons found at marked sites one day after marking. N = total number of animals observed.

that were present at the point of marking the following day had homed or simply had not moved during the night.

Acanthopleura granulata in low-energy zones which were not observed at their home the following day (only three) were observed from 5 to 35 cm away from their home. In moderate-energy zones, chitons which had not returned to their home by the following day were observed 5 to 500 cm from their home (Table 1). No distance measurements were done with high-energy-zone chitons because only a small percentage of the marked chitons in the high-energy zone were found the following day. The fact that marked chitons were not found within several meters of their home suggests that either these chitons could have traveled farther from their home than moderate-energy-zone chitons and relocated in areas that were inaccessible, or they were removed by predators or wave action. A *t* test detected no significant difference between the distances of low-energy-zone chitons and moderate-energy-zone chitons from their home. The reason no difference was detected could be due to the small number of individuals that did not home in the low-energy zone; this would make a significant difference difficult to detect. At night, chitons (*Acanthopleura granulata*) in moderate-energy zones ranged significantly

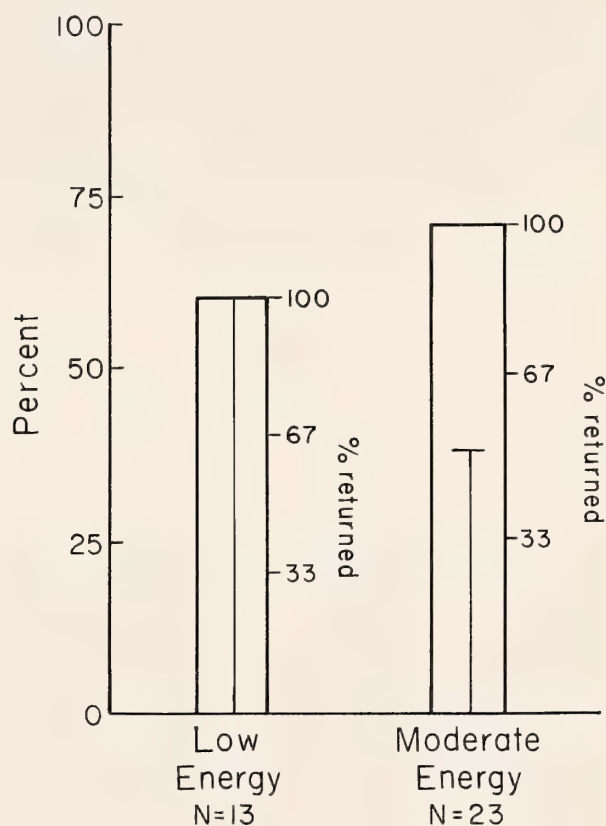


Figure 3

Percent of chitons observed away from site of marking at night in moderate- and low-energy zones. Solid line inside bar indicates percentage of these animals which had returned to the marked area the following morning.

farther (6–65 cm) from their home than chitons in low-energy zones (2–30 cm; $P < 0.05$) (Table 1).

Caloric values of the substrate at the moderate-energy site were significantly lower ($\bar{x} = 0.1767$ cal/mg) than the caloric value of the substrate at the lower energy site ($\bar{x} = 0.5056$ cal/mg; $P < 0.05$).

DISCUSSION

The observations in this study suggest that *Acanthopleura granulata* living in lower-energy zones may have a greater tendency to stay attached to their home than those living in higher-energy zones. When chitons in lower-energy zones do leave their home to graze, they tend to travel shorter distances and to have a greater tendency to return to their home than do chitons in moderate- and high-energy zones.

The reasons for development of homing in chitons are unclear. Several explanations, such as protection from dislodgment (LINDBERG & DWYER, 1983; COLLINS, 1977),

Table 1

Distance (cm) that chitons were found away from the point of marking (home) the night and day following marking. NS means *t* value not significant at *P* = .05.

	Day after marking	Night after marking
Low energy		
Range (cm)	5-35	2-30
\bar{x} (n)	18.3 (3)	12.00 (11)
Moderate energy		
Range (cm)	5-500	6-65
\bar{x} (n)	61.12 (32)	36.22 (9)
<i>t</i> value	1.37 (NS)	2.73

predator avoidance (WELLS, 1980), maximum utilization of food resources (MACKEY & UNDERWOOD, 1977), and protection from desiccation (VERDERBER *et al.*, 1983; COLLINS, 1977; and others) have all been suggested for other homing mollusks. It is unlikely that protection from dislodgment is an important reason for homing in Bahamian *Acanthopleura granulata* because chitons in high-energy zones, where dislodgment is more likely due to high wave activity, have a lesser tendency to home. Whether homing is an important mechanism for predator avoidance was not determined. However, little evidence of predation and few predators (except humans at some sites) were observed at any of the study sites, suggesting that homing may not be important for predator avoidance in the Bahamas.

It is also not clear whether Bahamian *Acanthopleura granulata* home for protection against desiccation. The fact that chitons home less in high-energy areas, which are frequently wetted by wave action, could indicate that homing may be an adaptation to prevent desiccation. However, because homing may be accomplished by olfaction and/or trail retracing (McFARLANE, 1981; COOK, 1979; THORNE, 1968), the reduced homing in high-energy areas may be caused simply by trails and olfactory stimuli being washed away by wave action. If homing is important for the prevention of desiccation, the loss of a trail to home could be of little consequence for chitons in high-wave-energy areas where desiccation is not a major problem.

The lower caloric food value of the moderate-energy substrate zones may explain the more frequent and more distant nighttime excursions of chitons (*Acanthopleura granulata*) in moderate- (and possibly high-) energy zones. Studies with filter-feeding bivalves (WINTER, 1978) and grazing winkles (*Littorina littorea* Linné, 1758) (NEWELL *et al.*, 1971) have shown that feeding effort (filtration rates or radular movement) tended to decrease as food became more available. For example, winkles tended to have higher radula movement rates when their food supply was lim-

ited on a temporal basis (NEWELL *et al.*, 1971). NEWELL (1979) suggested that when food availability was lower, feeding effort may have had to increase in order for the organism to continue to get enough food to sustain itself. In the case of the chitons examined in this study, the lower caloric value of the moderate-wave (and possibly high-) energy substrata may force animals in these zones to forage at more frequent intervals and to travel longer distances (increase grazing effort) in order to obtain the necessary calories to sustain themselves.

Other factors in addition to wave exposure or food availability may affect homing behavior in chitons. Elements such as inter-island variability, differences in substrate morphology, and differences in substrate productivity have not been addressed in this study and would be interesting subjects for future studies with *Acanthopleura granulata*.

ACKNOWLEDGMENTS

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Aspects of Reproduction in Some Enoploteuthid Squids from Hawaiian Waters¹

by

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Abstract. This study investigates aspects of reproduction of three enoploteuthid squid species, *Pterygioteuthis microlampas* Berry, *Pyroteuthis addolux* Young, and *Abraliopsis* sp., captured in Hawaiian waters during a 17-month, midwater-trawl sampling program. *Pterygioteuthis microlampas* differed from the other species in having smaller ova and higher relative fecundity. Juveniles of *P. microlampas* were most often caught in spring months, indicating a seasonal spawning tendency in this species. Seasonality of spawning in one or more species also was indicated by fall and winter peaks in enoploteuthid larval abundance. Although the majority of females in the larger size classes had mated prior to capture, only a minority of ova in any specimen were mature and the ratios of female gonad dry weight to total body dry weight were generally low, suggesting that full reproductive maturity was not observed in these specimens. In light of these results, net avoidance is considered, as is the possibility that partially spent females were captured. Also raised is the question of whether these species are able to spawn in more than one spawning season.

INTRODUCTION

APPROXIMATELY 50 species of pelagic squid are known to occur in Hawaiian waters (YOUNG, 1978). Most of these are small in size and low in abundance. Those most commonly captured in mesopelagic trawl samples are of the family Enoploteuthidae. Previous studies of enoploteuthid species in Hawaii have primarily involved their systematics (BERRY, 1914), vertical distribution (YOUNG *et al.*, 1980; YOUNG, 1978; ROPER & YOUNG, 1975), photobiology (YOUNG *et al.*, 1980; YOUNG, 1972, 1973), and occurrence in the diet of larger carnivores (KING & Ikehara, 1956; CLARKE, 1971). A few papers have treated aspects of reproduction of enoploteuthids occurring in temperate waters (*e.g.*, SASAKI, 1914; OKUTANI & MCGOWAN, 1969; PEARCY, 1965). However, the life histories and reproductive biology of the Enoploteuthidae remain largely unstudied.

The following study was undertaken to investigate fecundity, size at maturity, larval abundance, seasonality, and other aspects of reproduction of the three most commonly sampled enoploteuthid squid species in Hawaiian waters. Many of the results must be considered prelimi-

nary due to the sampling difficulties inherent in studies of this kind. Nevertheless, this study contributes original data that provide new insights into the life histories of these little-known squid species.

MATERIALS AND METHODS

This study is based primarily on specimens collected at approximately monthly intervals 20 km west of Oahu, Hawaii, between August, 1977, and October, 1978. Juvenile and adult enoploteuthids were collected in nighttime oblique samples with a 3-m Isaccs-Kidd midwater trawl (IKMT) and a 1.25-m diameter bongo net (BB). Larvae (≤ 5 mm dorsal mantle length) were taken primarily in standard bongo nets (SB) of 70-cm diameter. Each net was equipped with a flow meter and a time-depth recorder. The IKMT had a mouth area of 7.7 m² and a mesh of about 6 mm, except for a 1-m cod end of 333 μ m. The IKMT was towed at 2 m/s and was retrieved at 40–50 m/min. The average maximum depth reached was 325 m (± 30 m), and the average volume filtered per tow was 101×10^3 m³. The BB mesh was 2.5 mm. It was towed at about 1.75 m/s and retrieved at 40–50 m/min. The average maximum depth was 304 m (± 6 m), and average volume filtered per net was 9434 m³. The standard bongo was towed at 1 m/s and retrieved at a

¹ Hawaii Institute of Marine Biology Contribution No. 666.

Enoploteuthid Larval Abundance

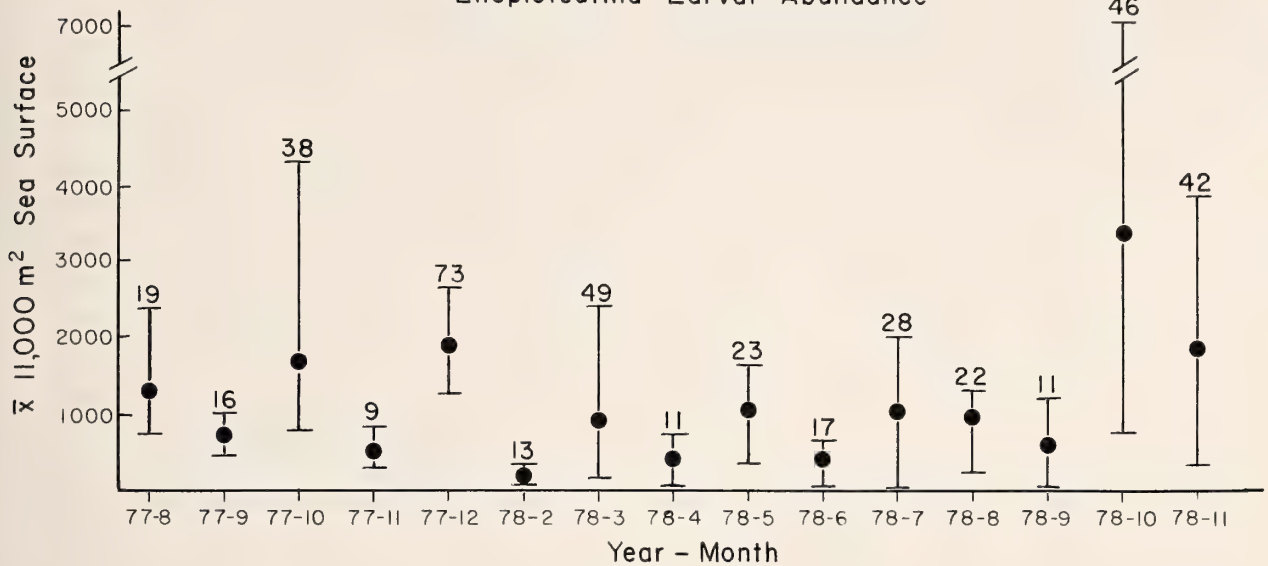


Figure 1

Monthly abundance estimates of enoploteuthid squid larvae ($\bar{x}/1000 \text{ m}^2$ of sea surface area) as determined by nighttime standard bongo tows. Mean values and ranges are indicated; n = number of larvae ($\leq 5 \text{ mm DML}$) captured.

rate of 60 m/min. The average maximum depth attained was 224 m ($\pm 33 \text{ m}$) and average volume filtered was 790 m^3 per net. For each tow, it was assumed that the entire sampled population occurred above the maximum depth attained by these nets. This assumption is supported by the vertical distribution study of YOUNG (1978). For each month, except January, 1978, when no samples were collected, 3-4 replicate IKMT tows, 2-4 standard bongo tows, and 2 large bongo tows were taken.

All samples were preserved in 10% formalin. Squid larvae from standard bongo tows were identified to family. For each SB tow, the number of enoploteuthid squid larvae per 1000 m^2 of sea surface area was estimated (after MAYNARD *et al.*, 1975) by multiplying the number of larvae captured by 1000 \times (maximum net depth/volume filtered).

Adult and juvenile enoploteuthids from BB and IKMT tows were identified to species, sexed, and dorsal mantle length (DML) measured. Specimens from IKMT catches were pooled by quarter to consider seasonal trends in size composition. K-S tests (SIEGEL, 1956) were used to estimate the significance of differences observed in the size frequency curves of *Pterygioteuthis microlampas* Berry, 1913, sampled in four seasons.

Ovaries were examined and extracted from adult and juvenile ($\geq 9 \text{ mm DML}$) specimens of *Pterygioteuthis microlampas*, *Pyroteuthis addolux* Young, 1972, and *Abraliopsis* sp. B (nomenclatural usage follows YOUNG, 1978). Gonad dry weight/total body dry weight ratios (G/S) were determined for all dissected specimens after drying for 24 h at 60°C.

Fecundity estimates were made for 10 or more of the largest specimens of each of the three species on the assumption that the larger specimens would contain the greatest numbers of mature ova. Individual fecundity was determined by direct count of all yolked oocytes. Oocytes were considered to be yolked if their nuclei were not discernible at 10 \times magnification. Relative fecundity, expressed as ova/g total dry weight, was used for interspecific comparisons. Mann-Whitney tests (ZAR, 1974) were used to estimate the significance of differences in relative fecundity.

Ova size-distribution frequencies were determined by manual dissection of the ovaries and examination of samples with a microscope. Several methods were used to sample the ovary in an effort to develop a reliable and accurate technique. In a total of nine specimens representing all three species, sections were examined from the most posterior and anterior ends of the ovary, and from the midsection. For most other specimens, only the posterior terminus of the ovary was examined. The entire ovary was examined in one specimen each of *Abraliopsis* sp. B and *Pterygioteuthis microlampas*. In three *Pyroteuthis addolux*, the entire ovary was gently teased apart and mixed, and several samples were examined.

RESULTS

The most commonly collected squid in 57 IKMT and 28 BB tows were the enoploteuthid species *Pterygioteuthis microlampas*, *Pyroteuthis addolux*, and *Abraliopsis* sp. B. One hundred and sixteen adult and juvenile ($\geq 9 \text{ mm}$

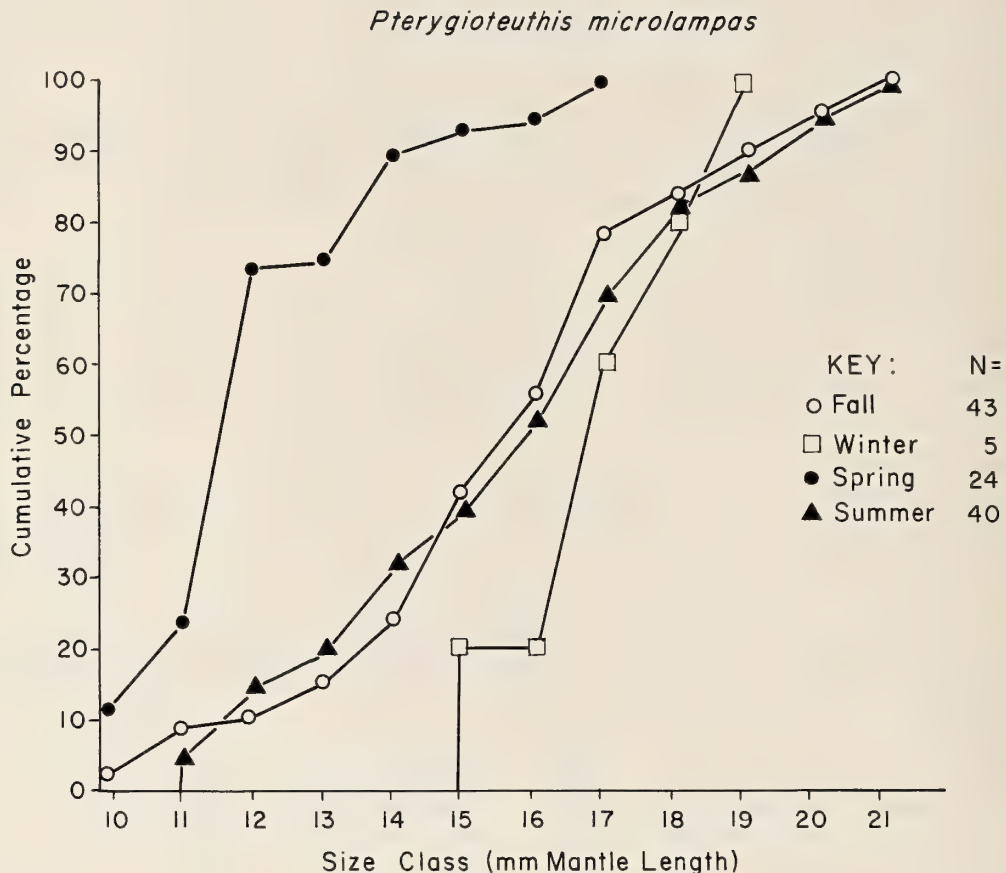


Figure 2

Cumulative size class percentages of *Pterygioteuthis microlampas* sampled by IKMT in four seasons. The spring size-class distribution differs significantly from each of the others ($P < .01$, K-S test); n = number of specimens captured.

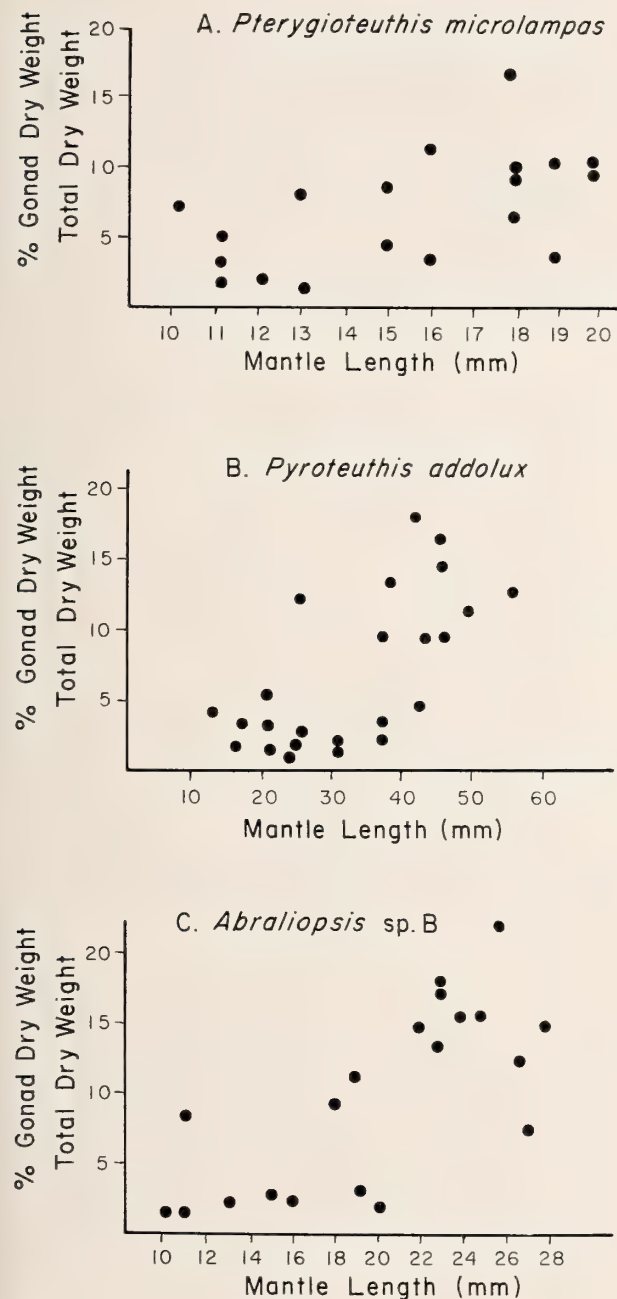
DML) *P. microlampas*, 88 *P. addolux*, 51 *Abraliopsis* sp. B, 48 *Pterygioteuthis giardi* Fischer, 1895, 26 *Abraliopsis* sp. A (after YOUNG, 1978), and 13 *Abralia trigonura* Berry, 1913, were collected.

Enoploteuthid larvae were present all year (Figure 1). The greatest abundances of larvae occurred during the months of October and December, 1977, and October and November, 1978, indicating the possibility of a seasonal spawning trend in one or more species. The large ranges observed in larval abundance estimates by the individual tows are probably due to the low average number of larvae captured per tow, but may also indicate patchiness of distribution.

The data for *Pterygioteuthis microlampas* (Figure 2) indicate that 90% were ≤ 14 mm in spring, that all sizes were more nearly equally represented in summer and fall, and that only animals ≥ 15 mm were found in winter. The size-frequency curve for spring differed significantly ($P < .01$, K-S test) from that of each of the other seasons,

but no significant differences ($P > .05$) were found among the other seasonal pairs. The absence of a significant difference between winter and spring or fall may have been the result of the smaller number ($n = 5$) of specimens collected in winter. *Pyroteuthis addolux* and *Abraliopsis* sp. B showed no coherent seasonal changes in size distribution.

The ratios of female gonad dry weight to total dry weight (G/S) were plotted against mantle length for the three species to estimate length at onset of reproductive maturity (Figures 3a, b, c). Increasing G/S ratios were not strictly correlated with increasing mantle length in any species, indicating that the onset of sexual maturity is not strictly size dependent, or that partially spent or spawning females may have been captured. The maximum G/S ratios for each species were found, not in the largest specimens, but in an 18-mm (DML) *Pterygioteuthis microlampas*, a 40-mm *Pyroteuthis addolux*, and a 26-mm *Abraliopsis* sp. B. The data for *P. microlampas* were the most scattered,



Figures 3a, b, c

Percent female gonad dry weight/total body dry weight plotted against dorsal mantle length for the three species studied.

perhaps due to a proportionally greater hydration error in the gonad weights of the small specimens during dry weighing.

The presence of spermatophores in the sperm receptacles of females of the larger size classes revealed that most had mated prior to capture. In *Pterygioteuthis microlampas*,

spermatophores were usually found in females ≥ 15 mm DML. Spermatophores were usually found in female *Pyroteuthis addolux* and *Abraliopsis* sp. B ≥ 35 and 20 mm DML respectively; however, an occasional specimen of *P. addolux* as small as 14 mm DML, an *Abraliopsis* sp. B of 11 mm DML, also were found bearing spermatophores.

Fecundity, ovum sizes, and G/S ratio data from the largest individuals captured are summarized in Table 1. *Pterygioteuthis microlampas* differed from the other species in its reproductive pattern of high relative fecundity and smaller ova. The number of yolked ova per gram dry body weight in *P. microlampas* was approximately $2.9\times$ that of *P. addolux*, and $2.8\times$ that of *Abraliopsis* sp. B. Both differences were statistically significant ($P < .05$, Mann-Whitney test). The largest ova of *P. microlampas* measured 60% of the maximum ovum diameter of the other species.

Ova size-frequency data (Figure 4) were similar for the three species regardless of the method used. Typically, the percentage of yolked ova ($\geq 300 \mu\text{m}$) found in the larger size classes increased with increasing G/S ratios. However, only a minority of ova fell within the largest size classes ($>700 \mu\text{m}$), even in individuals with the highest G/S ratios. Ova $700 \mu\text{m}$ or larger did not exceed 25% of the total number of yolked ova in any specimen. Non-yolked oocytes ($<300 \mu\text{m}$) accounted for an average of 63% (range 44–80%, $n = 10$) of all oocytes present. Therefore, only a very small percentage of the total number of oocytes present had developed into mature ova in any of the specimens examined.

The sex ratios for adult *Pterygioteuthis microlampas*, *Pyroteuthis addolux*, *Pterygioteuthis giardi*, and *Abraliopsis* spp. A and B did not differ significantly from 1:1 (99% confidence limits from TATE & CLELLAND, 1957). In the rarely captured *Abralia trigonura*, 10 of 13 specimens were females.

DISCUSSION

Although most of the adult female enoploteuthids examined in the present study had mated prior to capture, the generally low G/S ratios and scarcity of larger ova raise the question of whether full reproductive maturity was observed. Mating prior to full ova maturation has been reported for other squid species including *Loligo opalescens* Berry, 1911 (FIELDS, 1965) and *Todarodes pacificus* Steenstrup, 1880 (SOEDA, 1956 *vide* FIELDS, 1965, as *Ommastrephes sloani* Berry, 1912), and may also occur in Hawaiian enoploteuthids. According to FIELDS (1965), transfer of spermatophores in *L. opalescens* can occur "soon after the first few ova mature while the bulk of the gonad products are still unripe."

Despite the intensive sampling effort undertaken during the present study, the ripest females may have avoided capture. The problem of net avoidance by squid has been discussed by many authors (*e.g.*, HARDY, 1965; PEARCY, 1965; ROPER & YOUNG, 1975). Also, ROPER (1977) has

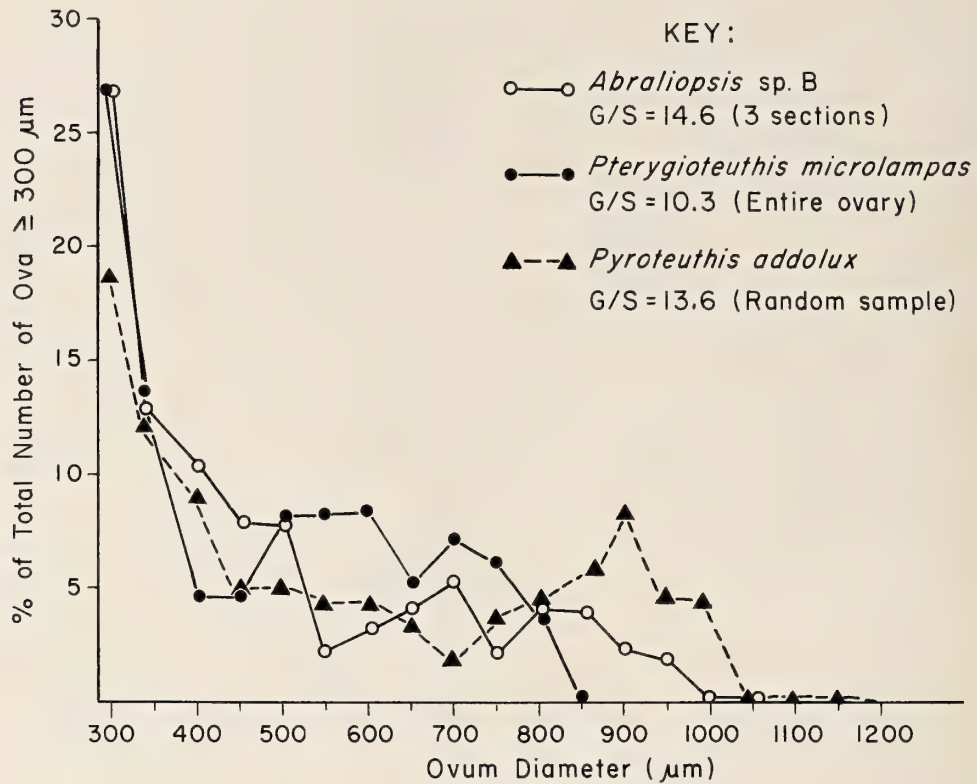


Figure 4

Typical ova size-frequency data for the three species studied. Distribution of ova expressed as the percentage of each size class relative to all ova $\geq 300 \mu\text{m}$. $n = 1$ specimen for each curve. Species, % gonad dry weight/total body dry weight (G/S), and sampling method are indicated for each curve.

demonstrated that cephalopod capture rates and catch compositions vary with different types of midwater trawls. Unfortunately, the bias of the present samples cannot be specified because there is no unbiased method with which to compare them. It is noteworthy that the extent of net avoidance by enoploteuthids seems to be less than that of other, more powerful species. In the present study, although the ommastrephid *Symplectoteuthis oualaniensis*

(Lesson, 1830) was frequently observed in the study area, neither juveniles nor adults of this fast swimming species were captured by trawl. In contrast, adult enoploteuthids were captured occasionally even in the SB plankton tows. Spawning specimens also may have avoided capture by migrating into deeper waters or shallow coastal waters to spawn. Shoreward spawning migrations are known in other squid species, including the enoploteuthid *Watasenia*

Table 1

Fecundity, ovum sizes and gonad dry weight/total dry weight ratios of three enoploteuthid species. (Data from largest individuals captured)

Species	n	Individual fecundity (No. yolked ova) $\bar{x} \pm \text{SE}$	Relative fecundity $\left(\frac{\text{No. yolked ova}}{\text{Gram dry body weight}} \right)$ $\bar{x} \pm \text{SE}$	Largest ovum diameter μm	Gonad dry weight Total dry weight $\bar{x} \pm \text{SE}$
<i>Pterygioteuthis microlampas</i>	11	259 ± 45.5	4641 ± 712.5	900	0.096 ± 0.010
<i>Pyroteuthis addolux</i>	10	1259 ± 205.5	1609 ± 168.5	1300	0.108 ± 0.014
<i>Abraliopsis</i> sp. B	10	476 ± 39.8	1675 ± 149.5	1300	0.141 ± 0.013

scintillans Berry (SASAKI, 1914). Alternatively, if these species mature rapidly and complete spawning in a short period relative to their life span, or form spawning aggregations, the chances of sampling them at this stage would be quite small.

Female *Loligo opalescens* can lose more than 50% of their dry body weight at spawning, approximately 40% being weight lost by the reproductive system (FIELDS, 1965). In a mature *Octopus maya* (Voss and Solis, 1966), 34% of the dry body weight was attributable to dry egg matter (VAN HEUKELEM, 1976). In this study, the highest G/S ratio was observed in a specimen of *Abraliopsis* sp. B. Only 21% of the dry body weight was attributable to dry ovary weight. The average G/S ratios recorded (Table 1) were much lower. The low G/S ratios could indicate that partially spent or spawning females were captured. However, in other species for which information is available, large numbers of non-yolked oocytes are not usually present in the ovaries of spawning individuals. SASAKI (1914) noted that most of the ova of spawning *Watasenia scintillans* were "mature" and that a comparatively small number of immature ova were imbedded in the ovarian tissue; unfortunately, his criteria of egg maturity were not specified. KNIPE & BEEMAN (1978) found that the ovaries of spawning *L. opalescens* differed cytologically from immature ovaries in lacking pre-oocytes, which were defined as oögonia smaller than approximately 59 μ m. In the present study, non-yolked oocytes predominated, a large proportion of which were comparable in size to the pre-oocytes of KNIPE & BEEMAN (1978).

If the most mature specimens were not avoiding capture, the low G/S ratios and ova size distributions could suggest that these species have the potential to spawn repeatedly. In most species of cephalopods, death follows mating and spawning (ARNOLD & WILLIAMS-ARNOLD, 1977). In the enoploteuthids studied, the non-yolked oocytes may represent potential modes of ova for future spawning. Further studies are clearly required before conclusions may be drawn concerning the reproductive habits of these species.

Young *Pterygioteuthis microlampas* were most often captured during spring months, indicating a seasonal spawning tendency in this species. Seasonal spawning in one or more species also is suggested by the peaks observed in enoploteuthid larval abundance during fall and early winter months. If the 10–12 mm juveniles of *P. microlampas* which dominate the spring catch were spawned in the fall, a growth rate of 1.8–2.0 mm/month can be conjectured for juveniles of this species. Seasonal spawning also has been reported in other enoploteuthid species. *Watasenia scintillans* spawns in Toyama Bay, Japan in late spring and early summer (SASAKI, 1914). In a study of pelagic cephalopods from Oregon, seasonal spawning in a species of *Abraliopsis* was suggested by the predominance of small individuals in summer trawl samples (PEARCY, 1965).

The higher fecundity of *Pterygioteuthis microlampas* relative to other Hawaiian enoploteuthid species may be re-

lated to its seasonal spawning tendency. The production of greater numbers of offspring could function to offset the risk of high mortality should spawning coincide with conditions not favorable to larval survival.

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Shell Repair Frequencies of Two Intertidal Gastropods from Northern California: Microhabitat Differences

by

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Abstract. *Tegula funebris* (A. Adams, 1854) and *Nucella emarginata* (Deshayes, 1839) from distinct microhabitats (surge channels, tidepool, and mussel bed) at Bodega Bay, California, were examined, and shell repairs enumerated. Frequencies of repair in samples of *Tegula* from each microhabitat were significantly different from each other. All samples of *Nucella* differed from each other except those from Surge Channel 2 and the mussel bed site. The significance of these results for interspecific comparisons of shell-repair frequencies is discussed.

INTRODUCTION

THE FREQUENCY OF shell repair in populations of intertidal gastropods has been used recently as an indicator of intensity of selection for antipredator traits (VERMEIJ, 1978, 1981, 1982a). Briefly, repairs are records of sublethal attacks by predators (or other shell-breaking agents), and snails that survive such attacks will contribute more progeny to subsequent generations than those which succumb (VERMEIJ, 1982b). Hence, where shell-repair frequencies are high, it is inferred that selection for antipredator traits is high. Shell breakage from agents other than predation should, by the same reasoning, select for some of the same shell characters. However, many morphological features are identified as defense primarily against predation, and scars left by predators are often distinguishable from other markings (VERMEIJ, 1978). Analysis of shell repair in various gastropods (VERMEIJ, 1978) and, in more detail, of terebrid snails (VERMEIJ *et al.*, 1980) reveal that repair frequencies are highest at low latitudes and, between oceans, in the Indo-West Pacific. These findings support other evidence that predation is a greater hazard to snails in the tropics than to those of temperate shores (VERMEIJ, 1978; ZIPSER & VERMEIJ, 1978; BERTNESS *et al.*, 1981; MENGE & LUBCHENCO, 1981). There are, however, possible problems with the use of shell-repair frequencies as an indicator of predation intensity, including small sample sizes, frequent reliance on museum collections, and microhabitat-related intraspecific variation in repair frequency. The purpose of this note is

to present data on intraspecific variation in shell-repair frequency.

MATERIALS AND METHODS

Tegula funebris (A. Adams, 1854) and *Nucella emarginata* (Deshayes, 1839) were collected in the intertidal zone adjacent to the Bodega Marine Laboratory (BML) near Bodega Bay on the northern California coast. The intertidal zone at BML consists of highly jointed granitic benches. Live snails were collected at four distinct microhabitats. Specimens of *Tegula* were collected at two surge channels and in a bed of the mussel *Mytilus californianus* Conrad, 1837. Specimens of *Nucella* were collected at the two surge channels, in the mussel bed, and also on a vertical rock surface near a mid-intertidal tidepool. Each snail was examined with a low-power binocular dissecting microscope. Shell repairs were identified as jagged relief on the surface of the body whorl. The extreme unevenness of scars distinguish them from growth lines, which may be prominent on these shells. Further, many scars are of a characteristic shape produced by the peeling action of the crabs (see VERMEIJ, 1978). Where ambiguity existed as to the origin of a marking, that shell was scored as not-scarred. Voucher specimens from each sample were retained.

RESULTS

Frequencies of shell repairs for *Tegula* were dramatically higher in the samples from the surge channels than in the

Table 1

Percentages of *Tegula* and *Nucella* shells with shell repairs, with sample size in parentheses. Code for microhabitats: surge channel 1 = SC1, surge channel 2 = SC2, mussel bed = MB, tidepool = TP.

	SC1	SC2	MB	TP
<i>Tegula</i>	49.6 (250)	28.5 (200)	3.8 (177)	—
<i>Nucella</i>	19.6 (234)	10.0 (200)	9.3 (236)	5.5 (200)

samples from the mussel bed: 123 of 250 and 57 of 200 shells from the surge channels had scars compared to 7 of 177 from the mussel bed (Table 1). Chi-square analysis shows that each sample differs significantly from the other two (Table 2). For *Nucella*, like *Tegula*, the samples from the surge channels had the highest repair frequencies, with the mussel-bed and tidepool samples next in descending order. However, only Surge Channel 1 was significantly different than the others (Table 2).

Interspecific comparison shows that *Tegula* is significantly more scarred in the surge channel microhabitats, whereas *Nucella* is more scarred in the mussel bed (Table 2).

DISCUSSION

These results show shell-repair frequencies can vary between microhabitats. To interpret interspecific differences in shell-repair frequencies meaningfully, a range of microhabitats should be sampled. For example, a possible misinterpretation based on mussel-bed samples would be that *Nucella* is more scarred than *Tegula*; whereas data pooled from several microhabitats show that *Tegula* is significantly more scarred ($\chi^2 = 79.2$, $P < 0.001$). Hence, discussion of the significance of differences in shell-repair frequencies should treat *Tegula* as the more scarred species. Although this study is not intended as a test of hypotheses of gastropod shell evolution, it is clear from the arguments outlined in the Introduction that one would expect selection for antipredatory traits to be higher for *Tegula*. However, *Tegula*, a typical trochid, possess few structural features identifiable as antipredatory. In contrast, *Nucella* has a narrow aperture and a short spire, both identified as defensive (VERMEIJ, 1978). This apparent discrepancy may be a result of an invalid comparison of phylogenetically distant species; morphological constraints and potential evolutionary responses may not be similar for both species.

At present I can only speculate on the source of variation in scar frequency reported here. The surge channel microhabitats might be more accessible to mobile predators (e.g., crabs and fishes) compared to mussel beds due

Table 2

Chi-square test with continuity correction of differences in shell-repair frequencies between each sample. Code for microhabitats as in Table 1, except prefaced by *T* (= *Tegula*) or *N* (= *Nucella*). All values are significant at $P < 0.05$ except where marked ns ($P > 0.05$).

	TSC1	TSC2	TMB	NSC1	NSC2	NMB	NTP
TSC1	—	19.7	103.3	46.2	78.3	91.8	100.8
TSC2	—	—	40.3	4.2	20.8	25.6	35.9
TMB	—	—	—	22.0	4.7	4.1	0.3 ns
NSC1	—	—	—	—	7.1	9.3	17.7
NSC2	—	—	—	—	—	0.006 ns	2.2 ns
NMB	—	—	—	—	—	—	1.74 ns

to unbroken connection with lower-intertidal and subtidal levels, and perhaps due to its horizontal aspect facilitating predator movement. For example, while diving in other nearby surge channels, I have observed the large rock crab *Cancer antennarius* Stimpson, 1856, to be abundant. Similar densities are expected in the surge channels reported on here. Further, wave action may at times be intense, resulting in nonpredator-induced shell breakage. Lower frequencies of shell repair in the mussel bed for *Tegula* and tidepool for *Nucella* may be due to refuge from predators and wave shock afforded by these microhabitats. The reversed trend of shell breakage frequency in the mussel bed remains an interesting problem. Probable durophagous predators in the mussel bed are the black oystercatcher, *Haematopus bachmani* Audubon, and the lined shore crab, *Pachygrapsus crassipes* Randall, 1839; however, no data are available on preferences of these predators for *Tegula* or *Nucella*.

Finally, some repair frequencies reported here are high compared with those reported for temperate and even some tropical snails. For instance, VERMEIJ *et al.* (1980) report average frequencies of 0.25–0.96 (where multiple scars on a shell are counted) for tropical terebrids, and 0.28 for temperate species. Frequencies reported for other temperate species are lower (VERMEIJ, 1978). The data presented here and elsewhere (REIMCHEN, 1982; VERMEIJ, 1982a) do not contradict conclusions about latitudinal predation patterns, but they do show that shell breaking agents can be locally intense in temperate as well as tropical gastropod assemblages.

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Morphological Divergence and Predator-Induced Shell Repair in *Alia carinata* (Gastropoda: Prosobranchia)

by

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Abstract. Morphological divergence of shell carina between protected harbor and exposed rocky cove populations of *Alia carinata* (Hinds, 1844) at Bodega Bay was documented by assigning and comparing keel ratings. The harbor population had a significantly higher frequency of highly keeled individuals than the cove population. Shell-scar frequency data provide evidence that predation intensity is greater in the harbor, and we suggest a relationship between morphological divergence and differential predation pressure.

INTRODUCTION

POLYMORPHISM HAS BEEN observed in geographically separated populations of many gastropod species (*e.g.*, KITCHING *et al.*, 1966; SPIGHT, 1973; KITCHING & LOCKWOOD, 1974; HELLER, 1976; VAN MARION, 1981; REIMCHEN, 1982). Specific morphs often seem to be particularly well adapted to their local environment (*e.g.*, KITCHING & LOCKWOOD, 1974). Compelling evidence for this assertion comes from studies of the defensive morphology of gastropods from sites with and without abundant predators. Where predators such as durophagous crabs are abundant, snail shells are thicker, more sculptured, or have narrower apertures (KITCHING *et al.*, 1966; HUGHES & ELLNER, 1979; REIMCHEN, 1982), traits identified as adaptations primarily against predation (VERMEIJ, 1978). The major evidence supporting a causal relationship between predator abundance and the presence of armor is that armored shells are more resistant to crushing forces (KITCHING *et al.*, 1966; KITCHING & LOCKWOOD, 1974; CURREY & HUGHES, 1982).

Alia carinata (Hinds, 1844) (= *Mitrella carinata*) is a small (<11 mm) columbellid gastropod found abundantly in the low intertidal zone of northern California (see MORRIS *et al.*, 1980). *Alia* is especially common on the seagrasses *Phyllospadix scouleri* (Hooker) and *P. torreyi* (Watson) on open rocky shores, while it is found on *Zostera marina* (L.) on soft substrates. Preliminary observations indicated that some specimens were noticeably more keeled at the shoulder of the body whorl and that the outer apertural

lip was more crenulated (Figure 1). In this paper, we document morphological divergence in *A. carinata* and present evidence suggesting the divergence is a result of differences in predation intensity between populations.

MATERIALS AND METHODS

Our study sites were a sheltered, soft bottom harbor in Bodega Bay, California, and a rocky cove (Horseshoe Cove) just outside of Bodega Bay. *Alia carinata* were collected at both sites by combing plants by hand from base to tip in May, 1982. Shell length from base to apex and greatest width perpendicular to the axis of coiling were measured to the nearest 0.1 mm with vernier calipers. To quantify extent of keeling, a standard set of morphotypes was assembled which typified the range of keeling observed in natural populations. Five individuals were selected, ranked by extent of keeling, and assigned keel values of 1 (least keeled) to 5 (most keeled) (Figure 1). Snails sampled from the harbor and the cove were assigned keel ratings corresponding to the morphotype they most closely resembled.

To quantify the frequency of shell scars, 475 harbor snails and 343 cove snails, collected in July, 1982, were examined with a binocular dissecting microscope under low magnification. Any obscuring epibionts were gently removed with a scalpel. Chipped outer lips, broken spires, and jagged blemishes extensive enough to interrupt normal growth lines were considered predator-induced scars. Eroded shell surfaces were not considered to be scars.



Figure 1

Dorsal (above) and apertural (below) views of *Alia carinata* showing extent of keeling. Keel ratings range from 1 (far left) to 5 (far right). Shell lengths of morphotypes vary from 7.4 to 8.1 mm.

RESULTS

Harbor *Alia carinata* had a significantly greater width-to-length ratio (harbor: 0.526; cove: 0.469; $F_{(1, 306)} = 224.10$, $P < 0.01$); however, harbor and cove samples were not

significantly different in shell length. Although keeled morphotypes were present in both populations, keel ratings were significantly greater for harbor *Alia* and highly keeled forms were absent from the cove habitat (Table 1).

Table 1

Extent of keeling of *Alia carinata* collected from rocky cove and soft-bottom harbor habitats. Distribution of keel ratings differ significantly between the two study sites (Kolmogorov-Smirnov Two Sample Test: DMAX = 0.7198; $P \ll 0.01$).

Keel rating	Cove <i>Alia</i>		Harbor <i>Alia</i>	
	Number	Percent	Number	Percent
1	117	67.24	13	9.70
2	42	24.14	13	9.70
3	15	8.62	48	35.82
4	0	0	42	31.35
5	0	0	18	13.43
Totals	174	100.00	134	100.00

The frequency of shell scars was significantly greater in the harbor. Of 475 harbor *Alia*, 164 (35.6%) had scars. Of 343 cove *Alia*, 51 (14.8%) were scarred (adjusted chi-square = 23.16, $P < 0.001$).

DISCUSSION

Our results document shell-morphology divergence between Bodega harbor and rocky shore populations of *Alia carinata*, and shell-scar data suggest that higher predation rates in the harbor may account for this divergence. Although we did not directly observe acts of predation on *Alia*, shell scars are records of past predation attempts, and shell-repair frequency is an indicator of predation intensity on a population (see VERMEIJ, 1982; VERMEIJ *et al.*, 1981). Correlation of morphological patterns and predation intensity is not sufficient evidence for the hypothesis that local selection by predators has resulted in interpopulation polymorphism. It must be shown that variation in predator-induced mortality actually exists (*i.e.*, a selective agent is acting), that present morphologies do in fact confer resistance to predation, and that local morphology has high heritability. Alternate explanations in the absence of this information include ecophenotypic effects and differential mortality among uniformly and widely dispersing larvae.

Our shell-scar data indicate that predation is a greater hazard to harbor snails than those from the cove. Thus, selection for defensive shell characteristics should be stronger in the harbor. Because *Alia carinata* lays egg capsules and has crawl-away larvae (D. Carlton, personal communication), immigration from populations lacking such selective pressure is unlikely. As a result, opportunity for divergence is enhanced (CURREY & HUGHES, 1982).

Evidence that keeled snails are more resistant to crushing is lacking. However, we have preliminary observa-

tions of prey selection by small *Cancer antennarius* (Stimpson), a predatory crab sympatric with both harbor and cove *Alia*. In 12 2-h feeding trials in which six keeled and six unkeeled snails were offered to starved *C. antennarius*, 30 unkeeled snails and 15 keeled snails were killed and consumed. In addition, 14 unkeeled snails were damaged, compared to only one keeled snail. These data are inconclusive, but suggest that keeled snails are less susceptible to crushing predation. The evidence that morphological divergence in *Alia* is related to predation is strong; however, ecophenotypic effects due to habitat differences such as water temperature and velocity, time of aerial exposure, and food availability cannot be ruled out.

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Thermal Effects on Some Mangrove Mollusks

by

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Abstract. The thermal tolerance to temperature of five species of tropical intertidal mollusks—*Coecella horsfieldi horsfieldi*, *Diplodonta cumingii*, *Melongena pugilina*, *Mytilus viridis*, and *Terebralia sulcata*—were studied. Heat coma, acute lethal temperatures, and 6-h median tolerance limits were used as measures of thermal tolerance. Each of these three indices produced a correlation between intertidal location and the sensitivity of the species to thermal stress.

INTRODUCTION

THE USE OF COASTAL waters for cooling in electricity generating plants is increasing with greater demands for power. A number of these power plants are located near estuaries and utilize estuarine water for cooling and discharging heated water at temperatures about 10 to 15 C° above ambient. Although at the moment thermal pollution is not critical, it is anticipated that in time to come, with more powerful conventional as well as nuclear power plants being built, thermal discharges could create problems to coastal ecosystems (NAYLOR, 1965).

In the tropics and in the South-east Asian countries where inland water resources are limited, many of these plants will be located on the coast and near mangroves. Thermal changes in the mangrove environment could also result from other sources, such as land development for agriculture and industries, which could change the temperature regime of surrounding waters.

Most studies on thermal effects have been conducted in temperate regions (NAYLOR, 1965; HEDGPETH & GONOR, 1969). One of the few conducted in the tropical region of South-east Asia was a study by MENASVETA (1976), who evaluated the thermal effects on marine fishes of the Gulf of Thailand.

Knowledge of thermal effects on the tropical mangrove ecosystem and the associated organisms is very limited. Our study contributes to this knowledge by investigating the effects of heated water on five intertidal mollusks found in the local mangrove mudflats of Singapore. The thermal tolerance to increased temperature of the bivalves *Coecella horsfieldi horsfieldi* (Gray), *Diplodonta cumingii* Hanley, and *Mytilus viridis* L., as well as the gastropods *Melongena pugilina* (Born) and *Terebralia sulcata* (Born), were investigated. Hereafter, these species will be indicated by their generic names.

MATERIALS AND METHODS

For each species, 12 batches of 10 individuals were placed in 400-ml glass beakers containing well aerated seawater (30 ppt) and placed in a thermostated water-bath that was maintained at the test temperature. At hourly intervals a batch of 10 was randomly selected, and the number that survived was noted. Mortality was determined by placing the treated animals back into seawater maintained at room temperature (25°C) and then testing for sensitivity responses of the foot or valve when the foot of the animal was pricked with a needle (SOUTHWARD, 1958). Animals that did not respond were considered dead.

The sensitivity test with the needle was also conducted on the animals 5 min after treatment. The heat coma point was defined as the lowest temperature at which no response was elicited initially from the animal but on returning the animal to room temperature full activity was regained.

Treatment temperatures used in the experiments ranged from 25 to 52.5°C at 2–3 C° intervals. These treatment temperatures for each species are given in Table 1. The animals were acclimated to room temperature (25°C) for 24 h before they were used in the experiments.

The survival curves for each species and at each treatment temperature were obtained by plotting the number alive against duration of treatment (Figure 1). After transforming these curves into linear form by plotting the probability of survival against the logarithm of treatment duration, the 50% survival times were extracted and a sensitivity curve for each species was drawn by plotting 50% survival time against treatment temperature (Figure 2). From this, the acute lethal temperature (ALT) was obtained. This is the temperature at which 50% of the animals will die instantaneously.

Another thermal tolerance index was determined from

Table 1
Treatment temperatures of five mangrove mollusks.

Species	Treatment temperatures °C							
<i>Coecella horsfieldi</i>								
<i>horsfieldi</i>	25	38	40.5	45	46	47.5	50	52.5
<i>Diplodonta cumingii</i>	25	33	35	40	41.5	43	45	47
<i>Terebralia sulcata</i>	25	38	40	43	45	47	49	51
<i>Melongena pugilina</i>	25	35	38.5	39.5	40.5	41.5	42.5	45
<i>Mytilus viridis</i>	25	35	37.5	38.5	39.5	41	43	45

the 6-h temperature-mortality curves ($_{6-h}TL_m$). The 6-h limit was chosen because most of these intertidal animals are seldom submerged for more than 6 h per tidal cycle in the natural environment.

RESULTS

Habitat of Test Organisms

Coecella, *Diplodonta*, and *Terebralia* are normally found in the upper intertidal zone of the mangroves, whereas *Melongena* and *Mytilus* are lower intertidal species.

Coecella is buried near the surface in sandbars located in the tributaries draining the mangrove swamp. *Diplodonta* is buried deeper in compact, moist mud, usually located between the roots of the mangrove plants, and this species is often found together with the peanut worm *Phascolosoma lurco* (Selenka & de Man). *Terebralia* is found along the muddy banks at the base of the mangrove plants among the pneumatophores.

Melongena frequents moist, muddy habitats and areas with large gravel and stones. *Mytilus* is found attached to solid substrata, such as poles or concrete pillars, farther away from the mangrove trees.

These intertidal mollusks are usually subjected to semi-diurnal tides and are submerged and exposed twice a day. The upper intertidal species are subjected to a longer duration of desiccation and solar radiation than the lower intertidal species. All are also subjected to fluctuating salinities which ranged between 25 and 30 ppt, the former at low tides and the latter at high tides.

Behavioral Responses to Heated Water

In general, all five species showed four phases of response when exposed to increasing degrees of heated water. At the lower temperature levels, the animals were active and responded readily to needle pricks. *Coecella* and *Diplodonta* showed vigorous burrowing movements of their muscular foot. Specimens of *Mytilus* produced byssus for attachment to the beaker and constantly opened and closed their valves. Active crawling was observed in *Melongena* and *Terebralia*. When pricked by a needle, both the bivalves and the gastropods showed their sensitivity by immediate withdrawal of the foot or closure of the valves.

Following this initial stage, a phase of lethargy was observed. Occasional movements were noted and the animals reacted slowly to needle pricks while still submerged in the heated water. Copious secretion of mucus was observed. After this phase the animals showed no reaction when pricked. This occurred at higher temperatures, and the animals apparently were in a state of heat coma. These animals, however, regained their sensitivity to needle pricks when they were transferred to room temperature seawater.

At the fourth and final phase, the animals were completely insensitive to needle pricks even after they were transferred into room temperature water. The tissues of these dead animals were tough and hard, whereas in the previous comatose phase, the tissues were soft, flaccid, and discolored.

Survival and Sensitivity to Heated Water

The survival curves for the five species are given in Figure 1. The usual sigmoid survival patterns were observed. The resulting sensitivity curves (Figure 2) showed linear relationships between the 50% survival time and the treatment temperature for all five species. *Coecella* showed a slight deviation from the linear pattern.

Coecella and *Terebralia* had the highest thermal tolerance followed by *Melongena* and *Diplodonta*. The least tolerant was *Mytilus*.

The acute lethal temperature points (ALT), the temperatures at which 50% of the test animals would die instantaneously, were obtained from the sensitivity curves (Table 2). The ALT were highest, and similar, for *Coecella* and *Terebralia*, about 50 and 49°C respectively. These species were closely followed by *Melongena* and *Diplodonta* with ALT of about 45°C. *Mytilus* had the lowest ALT, about 43°C.

The heat coma temperatures (HCT) for the five species are also given in Table 2. The highest HCT was observed for *Coecella* (40.5°C) followed by *Terebralia* (40.0°C) and *Diplodonta* (35°C). *Melongena* and *Mytilus* had the lowest HCT (32°C).

The order of thermal tolerance measured by the HCT is similar to that indicated by the ALT. A temperature

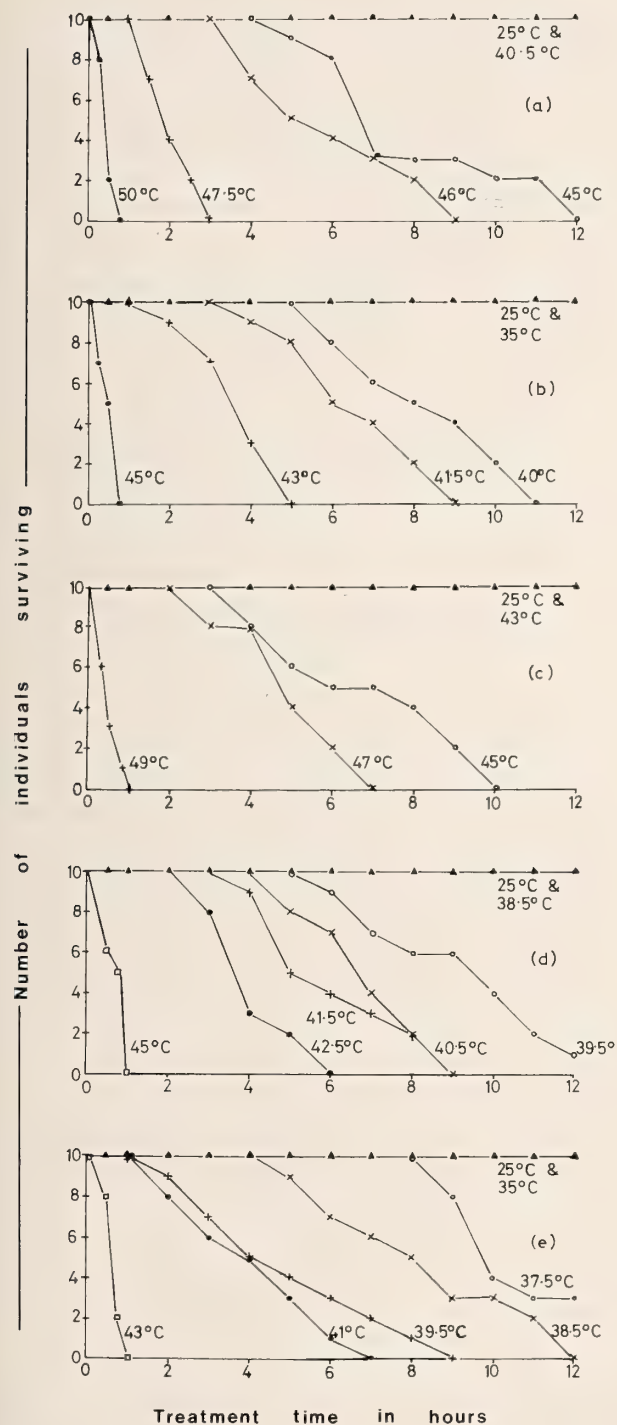


Figure 1

Survival curves of five species of mangrove mollusks subjected to different water temperatures. (a) *Coecella horsfieldi horsfieldi*, (b) *Diplodonta cumingii*, (c) *Terebralia sulcata*, (d) *Melongena pugilina*, (e) *Mytilus viridis*.

Table 2

Thermal tolerance values of five mangrove species of mollusks.

Species	Heat tolerance indices (°C)		
	Heat coma point	6-h TL _m	Acute lethal point
<i>Coecella horsfieldi horsfieldi</i>	40.5	45.8	49.7
<i>Terebralia sulcata</i>	40.0	44.9	49.4
<i>Diplodonta cumingii</i>	35.0	41.5	45.1
<i>Melongena pugilina</i>	32.0	41.2	45.4
<i>Mytilus viridis</i>	32.0	39.1	43.0

difference between the two indices of about 10 C° was observed for all five species.

The 6-h median tolerance limits, 6-h TL_m (Table 2), extracted from the 6-h temperature-mortality curves (Figure 3), showed the same order of thermal tolerance as those obtained from the other two indices. However, their temperature values were halfway between the heat coma and the acute lethal temperature points. The temperature differences were almost the same for all species (4–5 C°).

DISCUSSION

Information on the temperature tolerance and response of intertidal marine animals is of importance in assessing the biological effects of thermal pollution and changed temperature regimes in the aquatic environment. Studies on a wide range of intertidal species are available (NAYLOR, 1965). However, benthic mollusks are especially suitable for assessing the ecological effects of any thermal stress, because, unlike the more mobile species such as fishes, they are unable to move away from the affected areas. Studies on mollusks are found in EVANS (1947, 1948), DAVIS (1960), SANDISON (1967), MISCALEFF & BANNISTER (1967), HEDGPETH & GONOR (1969), and ANSELL (1973). Studies on tropical species have been conducted by LEWIS (1960, 1963, 1971) and ANSELL & TREVALLION (1969).

In many countries, changes of temperature in the mangrove environment could result not only from direct thermal discharges of electricity generating stations but also from industrial heat waste, dams, irrigation practices, and other land use activities such as housing and industrial development nearby. In order to evaluate these changes and their potential effects on the mangrove ecosystem, the temperature tolerances of the resident organisms need to be investigated first.

Our results showed that the tolerance of high temperature by the five mollusk species is related to their vertical distribution along the shore. All three heat-tolerance indices indicate that the upper intertidal species, *Coecella* and *Terebralia*, were more tolerant than the lower inter-

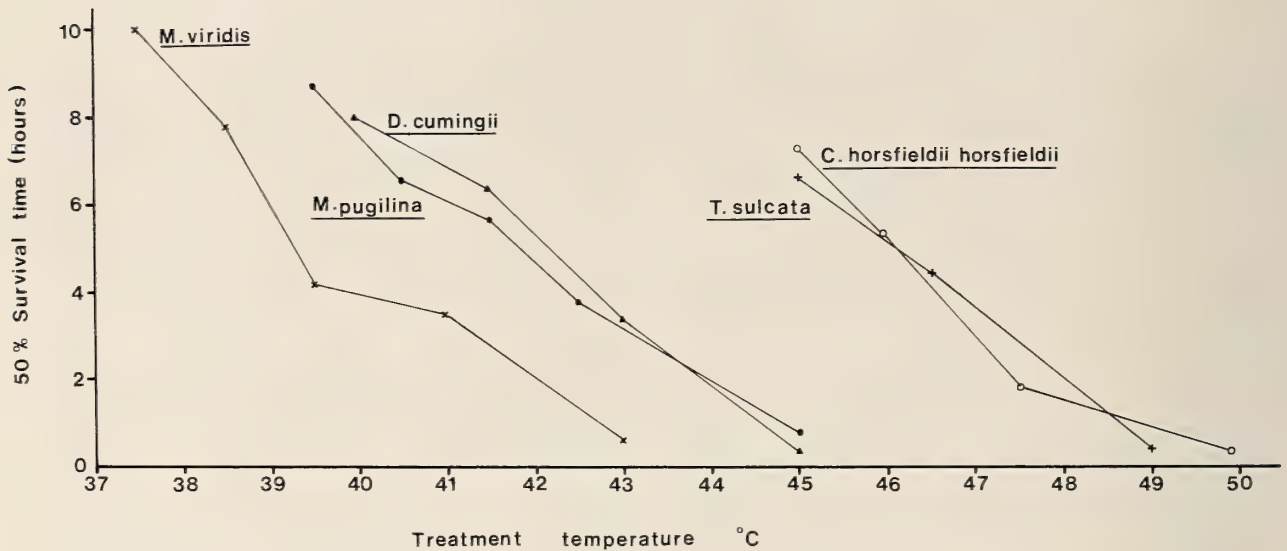


Figure 2

Temperature sensitivity curves of five species of mangrove mollusks. The 50% survival times (hours) were obtained from log-probit transformation of the survival curves.

tidal species, such as *Melongena* and *Mytilus*. *Diplodonta* is an exception: although it inhabits the upper intertidal, it has lower heat tolerance than the above two upper intertidal species. This is probably due to the fact that they are adapted to live deeper in the mud substratum where temperatures are normally lower than on the surface. A

similar correlation with vertical zonation has been shown by other investigators (EVANS, 1948; BULLOCK, 1955; GUNTER, 1957; SOUTHWARD, 1958; SANDISON, 1967). They also have shown that thermal death points were correlated with the order in which animals were zoned on the shore.

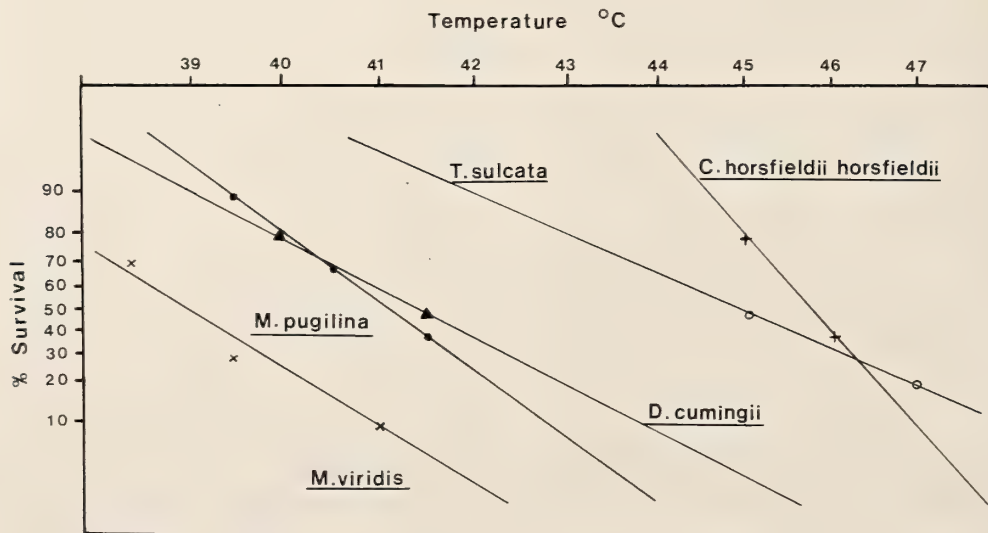


Figure 3

Six-hour temperature-survival curves of five species of mangrove mollusks. % survival on probit scale.

Of the five species investigated, *Mytilus* consistently showed the lowest heat-tolerance temperature indices. Therefore, it should be the indicator species for evaluating any thermal change, and their heat-tolerance temperatures used as a basis for thermal pollution control of the mangrove ecosystem.

The three heat-tolerance indices used in this study were the heat coma temperature (HCT) following SOUTHWARD (1958), the 6-h median tolerance limit ($_{6-h}TL_m$) using the usual bioassay methods, and the acute lethal temperature (ALT) derived from the sensitivity curves. If comparison of relative thermal tolerance among the species is required, it can be seen that any of the three indices could be used.

Based on the above, then 31–32°C should be the water temperature criterion for the protection of the mangrove ecosystem, and the decline in population size of *Mytilus*, or its disappearance, should be one of the indications of thermal stress to the ecosystem.

The temperature of the natural environment is between 28.5 and 30.5°C (THAM *et al.*, 1970). Therefore, the thermal stress temperature points of the species studied were very close to the ambient temperature of their natural environment. These tropical mangrove mollusks are living very near to conditions of thermal stress. A small increase of 2–3 C° in water temperature would be detrimental to them and the mangrove ecosystem. Here, as well as elsewhere, it seems that tropical organisms have low ranges of temperature tolerance (MOORE, 1972).

In conclusion, it can be seen that in terms of thermal stress, the mangrove is a fragile ecosystem. A slight temperature increase definitely would affect it. In developing the mangroves for aquaculture, agriculture, industrial or other land use, careful consideration, therefore, should be given to the changes in temperature regimes of the adjacent waters.

ACKNOWLEDGMENTS

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Barnacle Attachment on Live *Nautilus*: Implications for *Nautilus* Growth Rate

by

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Abstract. Attachment of the barnacle *Chirona tenuis* (1.8 cm in height) onto the mid-venter of a juvenile *Nautilus pompilius* (10.7 cm in diameter) during its life permits observations on the secretory reaction of the nautilus to the presence of the barnacle and provides an estimate of the growth rate of *N. pompilius* in nature. The nautilus secreted a thick, multilayered, black film interleaved with aragonite deposits in an attempt to overgrow the barnacle; the aragonite had a spherulitic-prismatic microstructure. The age of the barnacle provides a *minimum* estimate of the rate of growth of the last nautilus whorl. Growth band counts on three wall plates average 680. If growth band formation is presumed to be semidiurnal, based on field and experimental data for other barnacles, the age of the barnacle is 340 days and represents a minimum estimate of the rate of growth of the last nautilus whorl. Judging from the spacing of chambers, about 16 chambers probably formed during this time yielding a minimum average of about 21 days per chamber.

EPIZOA ON THE SHELLS of live *Nautilus* are not uncommon and typically consist of serpulid polychaetes near the umbilicus or on the shell flanks and venter (SEILACHER, 1982). The absence of more extensive premortal incrustation may be explained by the mobile life style of *Nautilus* (STENZEL, 1964), its smooth shell covered with a thin, organic periostracum (BOTTJER, 1981), and possibly some antifouling behavior. Barnacle attachment is rare but has been observed on live *N. belauensis* from Palau (W. B. Saunders, personal communication) and on live *N. pompilius* from Fiji (B. A. Foster, personal communication).

While studying collections at the Museum of Comparative Zoology, Harvard University, I discovered a small shell of *N. pompilius* (M.C.Z. No. 138167), 10.7 cm in diameter, with a large barnacle attached to its dorsum (Figures 1, 2). The barnacle, 1.8 cm in height and 1.9 cm in diameter, has been tentatively identified by B. A. Foster from photographs as *Chirona tenuis* (Hoek). This species lives in the Indo-West Pacific and elsewhere to depths of 500 m, approximating the maximum depth of *N. pompilius*, and often occurs on the shells of gastropods (NEWMAN & ROSS, 1976, p. 50, and references therein). The nautilus was collected off Golo Island, Mindoro, Philippines, and, although other details of collection are not available, incrustation was evidently premortal as the nautilus was in the process of overgrowing the barnacle. However, the

large size and position of the barnacle impeded further growth of the nautilus and may have affected its swimming and buoyancy capability. Aside from curiosity, this occurrence permits two further inquiries: documentation of the secretory reaction of the nautilus to the presence of the barnacle, and estimation of the growth rate of *Nautilus* in nature. The barnacle contains in its shell a record of its growth. By deciphering this record, an estimate of the age of the barnacle can be obtained which in turn permits an estimate of the growth rate of the nautilus.

Secretory Reaction to the Barnacle

On the dorsal part of its shell, *Nautilus* secretes a black layer or band presumably deposited by a portion of the mantle fold (JOUBIN, 1892). The black layer conforms to the shell surface, dampening out growth lines and shell irregularities. Epibionts such as serpulid worm tubes are neatly covered with a slight thickening of the black deposit. The black deposit is itself continuously overlain by an advancing layer of nacre as the animal grows, leaving only the leading centimeter or so of the black layer free of nacre (STENZEL, 1964). Thus, the black layer apparently serves to enshroud epibionts and, as JOUBIN (1892) suggested, to provide a more uniform surface for nacre deposition.

In the nautilus specimen studied, these functions were put to a severe test by the presence of the barnacle. The black layer extended onto the shell flanks and overgrew the lower edges of the barnacle walls. The black layer was thick and multilayered and was interspersed with deposits of aragonite which exhibited a botryoidal appearance under low magnification (Figure 3). Under scanning electron microscopy, these deposits revealed a spherulitic-prismatic microstructure composed of radiating crystals about 70 μm in length (Figure 4). This increase in secretory activity near the barnacle was not matched by any shell thickening at the apertural margin nor any reduction in the spacing of the last chamber (Figure 5).

Barnacle Age and *Nautilus* Growth Rate

Using epibionts that grew during the lifetime of their host to speculate about the growth rate of the host has been attempted for extinct ammonites by SCHINDEWOLF (1934). Although *Nautilus* is extant, information about its growth rate in nature, especially in juvenile animals, is sparse. DENTON & GILPIN-BROWN (1966), based on theoretical rates of gas-pressure build-up in newly formed chambers of *Nautilus macromphalus*, inferred a constant 14-day periodicity between septal formation, a figure later regarded as a minimum by COLLINS *et al.* (1980). *Nautilus macromphalus* maintained in aquaria have yielded estimates of 1–4 months between septal formation (MARTIN *et al.*, 1978; WARD *et al.*, 1981). The first estimates of the growth rate of *Nautilus* in nature, based on the activity ratio of two naturally occurring radionuclides incorporated into the shell during growth, yielded times of 25 and 75 days between septal deposition in two juvenile *N. pompilius* 8.4 cm in diameter (COCHRAN *et al.*, 1981).

Determination of the age of the barnacle attached to *N. pompilius* provides another means of estimating the natural growth rate of *Nautilus*. The barnacle settled almost exactly on the mid-line of the shell with its carinal plate oriented in the adapical direction of nautilus growth. Subsequent growth of the barnacle favored a bending toward the left flank of the nautilus and the parietal plates are shorter on this side. The basal disk is calcified and measures 1.9 cm in diameter. Below it on the shell surface, approximately 28 asymmetrically skewed concentric bands radiate from the original attachment site.

The age of the barnacle yields a *minimum* estimate of the rate of growth of the last nautilus whorl. The reasons are outlined below.

- (a) Depending on the position of the barnacle relative to the aperture at the time of settlement, no more than a full whorl of nautilus growth would have had to elapse before reaching its present position at the time of incipient overgrowth. According to SEILACHER (1960), a barnacle will settle on an inclined substrate with its carinal plate on top. Based on the orientation of *Chirona* (see above) and the living position of *Nautilus*,

the barnacle probably settled on the venter at some distance behind the aperture, facing into the direction of swimming. Therefore, less than a full whorl of nautilus growth would have had to elapse before reaching its present position.

- (b) Because the barnacle grew in both the adapical and adoral directions of nautilus growth, the nautilus actually encountered it about 6 mm or a few degrees of arc ($\sim 10^\circ$) adapical of its original attachment site. Therefore, at most, a little less than a full whorl of nautilus growth would have had to elapse.
- (c) Because the details of collection are lacking, it is possible that the barnacle died some time before the nautilus began to overgrow it. In this case, the age of the barnacle would definitely be less than the time of formation of the last whorl.

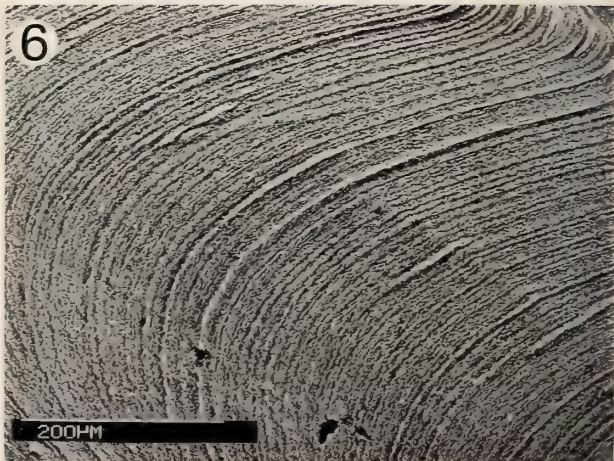
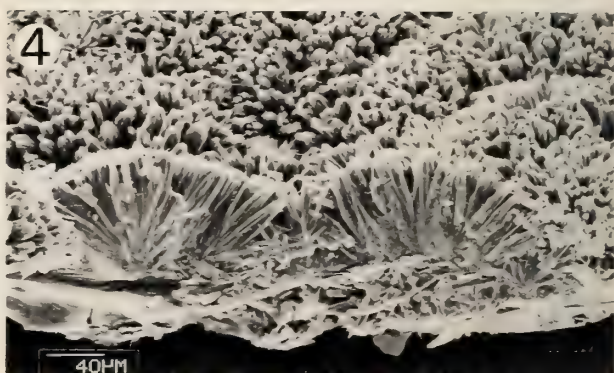
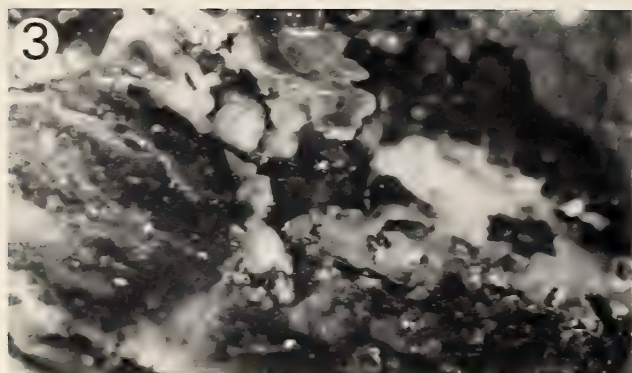
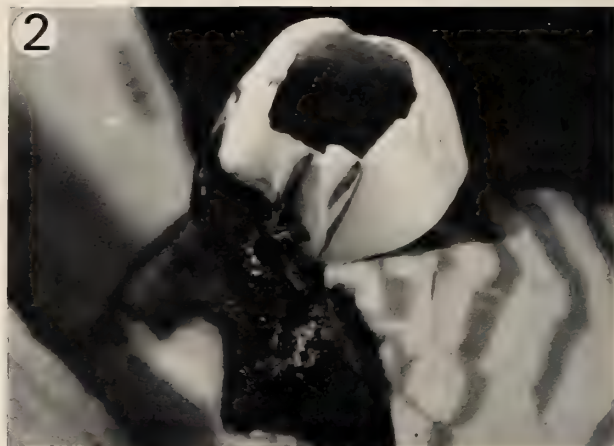
Determining the age of the barnacle presents its own problems. The most reliable growth information is contained in the form of internal growth bands visible in thin sections of the parietes (BOURGET, 1980). Observations on balanoids reveal that growth bands are present in the outer and inner layer (sheath) of the parietes and are wide enough for counting (BOURGET, 1980). Interpretations of growth-band periodicity are based almost exclusively on field and laboratory experiments on intertidal and shallow subtidal forms, principally *Semibalanus balanoides* and *Elminius modestus*. However, regardless of environmental conditions, including total darkness and continuous immersion, the production of growth bands is semidiurnal (BOURGET & CRISP, 1975a, b; BOURGET, 1977, 1980). In fact, BOURGET (1980) speculates that semidiurnal growth band formation may be under endogenous control.

"1.) semidiurnal bands are observed subtidally in newly metamorphosed animals; 2.) the production of semidiurnal bands is immediate after metamorphosis; 3.) the production of semidiurnal bands cannot be arrested in uniform conditions in the laboratory; 4.) bands [are] observed in subtidal species (Bourget, 1977); and finally 5.) bands are also observed in the deep-sea *Bathylasma coralliforme* sampled at a depth of 7,000 m in Ross Sea, Antarctic."

Based on these observations I will presume that the production of growth bands in *Chirona tenuis* is semidiurnal.

The growth band record in *C. tenuis* was examined on radial cross sections through three of the parietes. The wall plates were sectioned, polished, etched for about 4 minutes with EDTA, and replicated with acetate. The acetate peels were examined at 200 \times magnification with transmitted light. Growth bands were counted on the inner layer (sheath) of the parietes as suggested by BOURGET (1980), and varied in width from 5 to 11 μm (Figure 6). Growth bands were counted by three independent observers, and the results are tabulated in Table 1. The counts for all three parietes are similar and average 680 bands.

Presuming semidiurnal formation of growth bands, the



Explanation of Figures 1 to 6

Figure 1. The barnacle *Chirona tenuis* attached to the shell of *Nautilus pompilius* (MCZ No. 138167). Incrustation was pre-mortal as the nautilus was in the process of overgrowing the barnacle. The nautilus measures 10.7 cm in diameter; the barnacle measures 1.8 cm in maximum height.

Figure 2. Close-up of Figure 1 showing the black layer deposited on the wall of the barnacle. The carinal plate points in the adapical direction of nautilus growth.

Figure 3. Botryoidal deposits of aragonite interlayered with the black material (magnified 17.5×).

Figure 4. Spherulitic-prismatic microstructure of aragonite deposits in Figure 3.

Figure 5. X-ray photograph of nautilus (with barnacle removed) showing regular spacing of septa.

Figure 6. Scanning electron micrograph of growth bands in *Chirona tenuis* seen on an acetate replica of a radial cross section through the inner layer (sheath) of a wall plate. Growth bands measure 5 to 11 μm.

Table 1

Counts of growth bands in three wall plates of
Chirona tenuis (Hoek).

	Plate 1	Plate 2	Plate 3
	709	665	680
	682	669	684
	687	647	673
	683	686	684
	709	656	660
	706		696
Average	696.0	664.6	679.5
Standard deviation	13.30	14.67	12.13
Average all three plates		680.0	
Standard deviation		15.71	

age of the barnacle is 340 days. As explained, this figure represents a minimum estimate of the rate of growth of the last nautilus whorl. Chambers in this specimen are fairly regularly spaced and average 22° in angular arc (Figure 5); approximately 16 chambers would have formed during the growth of the last whorl. Therefore, the minimum average time of chamber formation for these 16 chambers is about 21 days. This figure is an average and does not imply a constant periodicity. It compares favorably with other estimates of natural growth rate based on growth of the last 6–9 chambers in two juvenile *N. pompilius* (COCHRAN *et al.*, 1981).

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Distribution and Abundance of *Caecum cornucopiae* (Gastropoda: Prosobranchia) on *Cladophora crystallina* Mats in a Bahamian Salt Water Lake

by

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Abstract. The minute gastropod *Caecum cornucopiae* (Gastropoda: Prosobranchia) was found in large mats of the fine, filamentous green alga *Cladophora crystallina* in Sweetings Pond, a salt water lake on Eleuthera Island, Bahamas. *Caecum cornucopiae* abundance decreased significantly between the top, middle, and bottom algal layers ($P \leq 0.05$). From collections made over a four-week period, five stages of shell growth were recognized. Stage correlated with aperture diameter ($r = 0.92$, $n = 109$) and was used as a measure of relative age. Stage-frequency distribution varied between the top, middle, and bottom layers of the *C. crystallina* mat. Stage-frequency distribution also varied with water depth, with a higher percentage of Stages I and II (juveniles) in deeper (7 m) water. Shallow water (0.5 m) contained a more uniform stage distribution. *Caecum cornucopiae* was found in abundance in the gut of a small brachyuran crab, and was also consumed by the fish *Eucinostomus lefroyi*.

INTRODUCTION

THE CAECIDAE IS A poorly known family of prosobranch gastropods (MOORE, 1972). Adults rarely exceed 3 mm in length and are easily overlooked. Shell growth is unusual, with immature stages passing through a planospiral protoconch followed by a loose helix before maturation when the shell becomes a gentle curve in one plane.

The literature on this family is scant and deals primarily with taxonomy and distribution (WARMKE & ALMODÓVAR, 1963; SWEDMARK, 1964; ARNAUD & POIZAT, 1979). MOORE (1972) presents systematic and ecological notes on the Caecidae from St. Croix, U.S. Virgin Islands. He reports that *Caecum cornucopiae* Carpenter, 1858, is a tropical, stenohaline species found near coral reefs and in lagoons where salinity does not decrease during fresh-

water runoff. This species has been found in the Bahamas, southern Florida, the western Caribbean, Puerto Rico, Jamaica, and the Lesser Antilles.

This report describes the habitat, distribution, and predators of a population of *Caecum cornucopiae*. Observations on the stages of shell growth are also included.

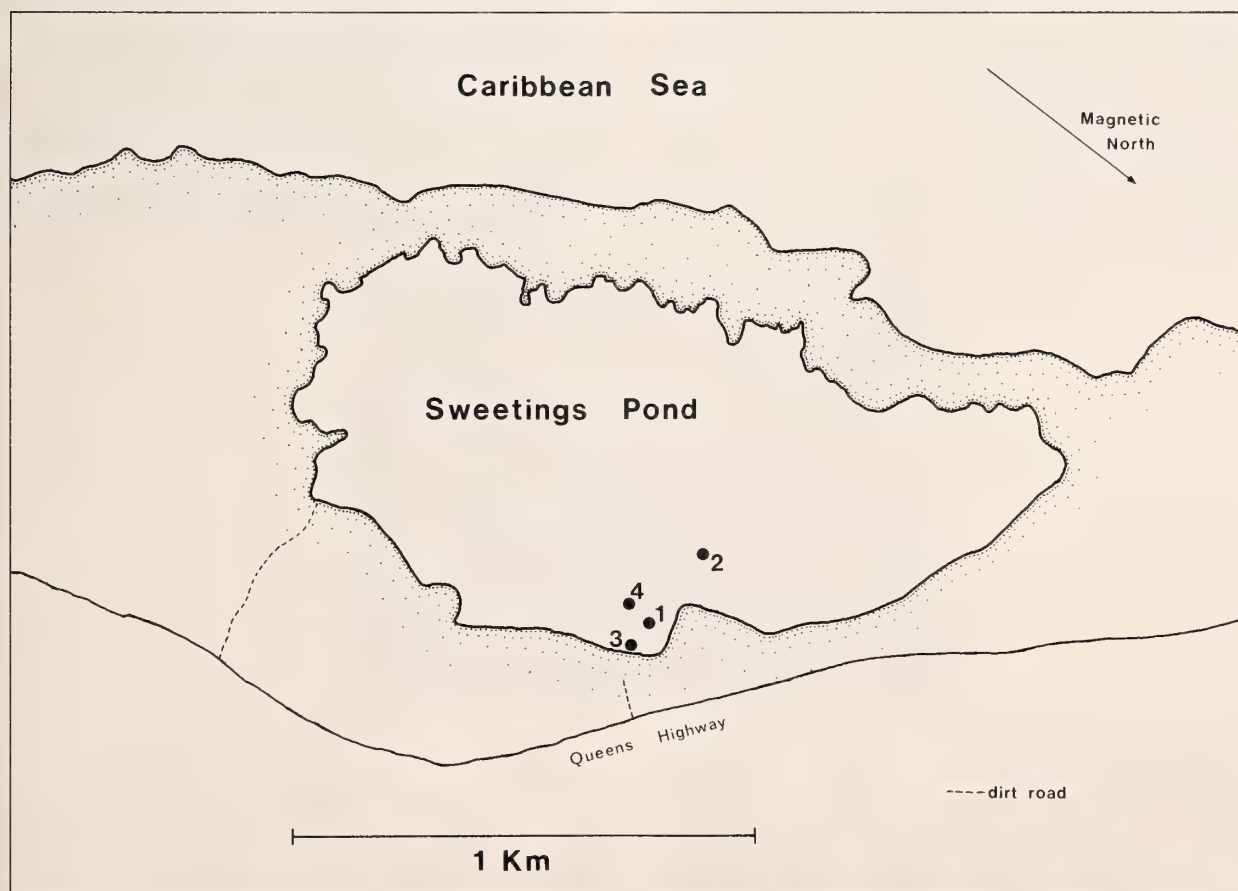
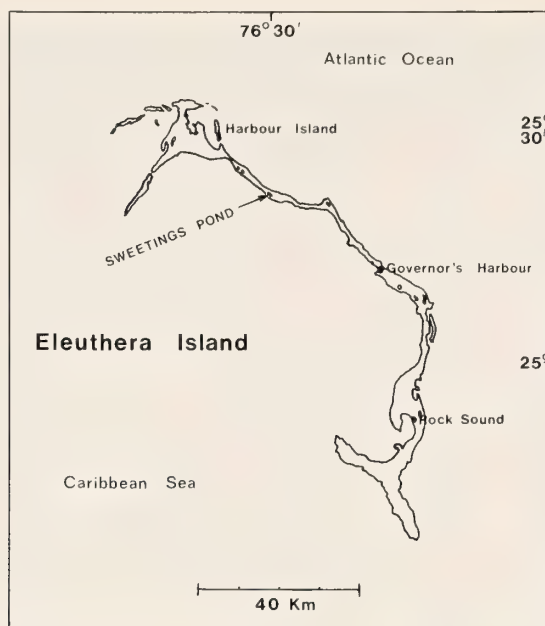
MATERIALS AND METHODS

Description of Study Site

Sweetings Pond (Figure 1) is an enclosed, salt water lake measuring 1.5×0.75 km, with a maximum depth of approximately 16 m. It is presumed to be connected to the Caribbean Sea through an underground cavern. Tidal amplitude in the pond is less than 10 cm. Ranges for

Figure 1

Location of the study site, Sweetings Pond, Eleuthera, Bahamas. Numbers in small-scale (bottom) map refer to sampling stations.



temperature (24–28°C), dissolved oxygen (6–7 mg/l), and salinity (36–38 ppt), all are similar to those of the Caribbean Sea. Currents are insignificant, although turbidity during the spring of 1982 was high: a Secchi disk held horizontally was not visible beyond 441 cm.

Mats of *Cladophora crystallina* (TAYLOR, 1960) were found at depths from 1 to 6 m around the perimeter of the pond, but their areal coverage varied. The alga often formed a solid mat up to 114 cm thick between 3 and 5 m, and occurred as patches in shallower and deeper locations.

Three stations were sampled (Figure 1). Station 1 was located in the middle of approximately a one-half hectare of algal mat, interrupted by occasional patches of sediment 2–3 m in diameter. Station 1 was over 5 m away from any sediment, and it is assumed that sediment fauna did not interact with mat fauna at Station 1; water depth was 2.5 m. Stations 2 and 3 were within 0.5 m of the sediment on patches of *C. crystallina* covering less than 3 m², at depths of 7 and 0.5 m, respectively.

Methods

Temperature was measured in and above the mat of *Cladophora crystallina* at Station 1 ($\pm 1^\circ\text{C}$). Dissolved oxygen was determined using a Hach field kit (model OX-2P, with a precision of 1 mg/l) at the bottom, middle, and top of the algal mat, as well as 1.5 m above the mat.

The shell-aperture diameter of 109 *Caecum cornucopiae* was measured with an ocular micrometer to the nearest 0.01 mm. Aperture diameter was thought to reflect relative age as it must increase as the animal grows. Five stages of shell formation were recognized based on protoconch presence or loss, the amount of helical coiling, and the loss of posterior shell sections.

The stage-frequency distribution of *Caecum cornucopiae* at the top, middle, and bottom of the algal mat was examined at Station 1. Each layer was sampled at three sites, with six replicates per site. Because sampling was destructive to the mat it was impossible to sample all three layers at one site. All sampling occurred within a 3-m radius of the Station 1 buoy. Sites were located adjacent to or beneath (for the middle and bottom layers) a $\frac{1}{4}$ m² quadrat that was released at the water surface and allowed to drift haphazardly to the mat. Thickness of the algal mat at each sampling site was measured prior to sampling. Samples were collected by holding the halves of a tea ball 50 mm apart and pressing them into a vertical wall of algae to a depth equal to the tea ball diameter. The tea ball halves were then brought together enclosing a cylinder of algae with a volume of 61.3 cc. Each sample was sorted under a dissecting microscope for enumeration of *C. cornucopiae* stages, as well as for the identification and enumeration of all other species. Crustaceans were not identified further due to taxonomic difficulties. Because the algal mat became compressed with increasing thickness due to the weight of overlying layers, displacement vol-

umes of all algal samples were recorded after the algae had been blotted dry. This allowed standardization of all enumerations to numbers per volume of *Cladophora crystallina*.

At Stations 2 and 3, a handful of top-layer algae was collected for stage-frequency comparisons of *Caecum cornucopiae* at different water depths. Algae were sorted until the first 60 or more individuals were assigned to stage classes.

Gut contents of large, algal mat fauna, as well as those of three species of fish seen over the mats, were examined to determine to what extent any of these species was utilizing *Caecum cornucopiae* as a food source.

RESULTS

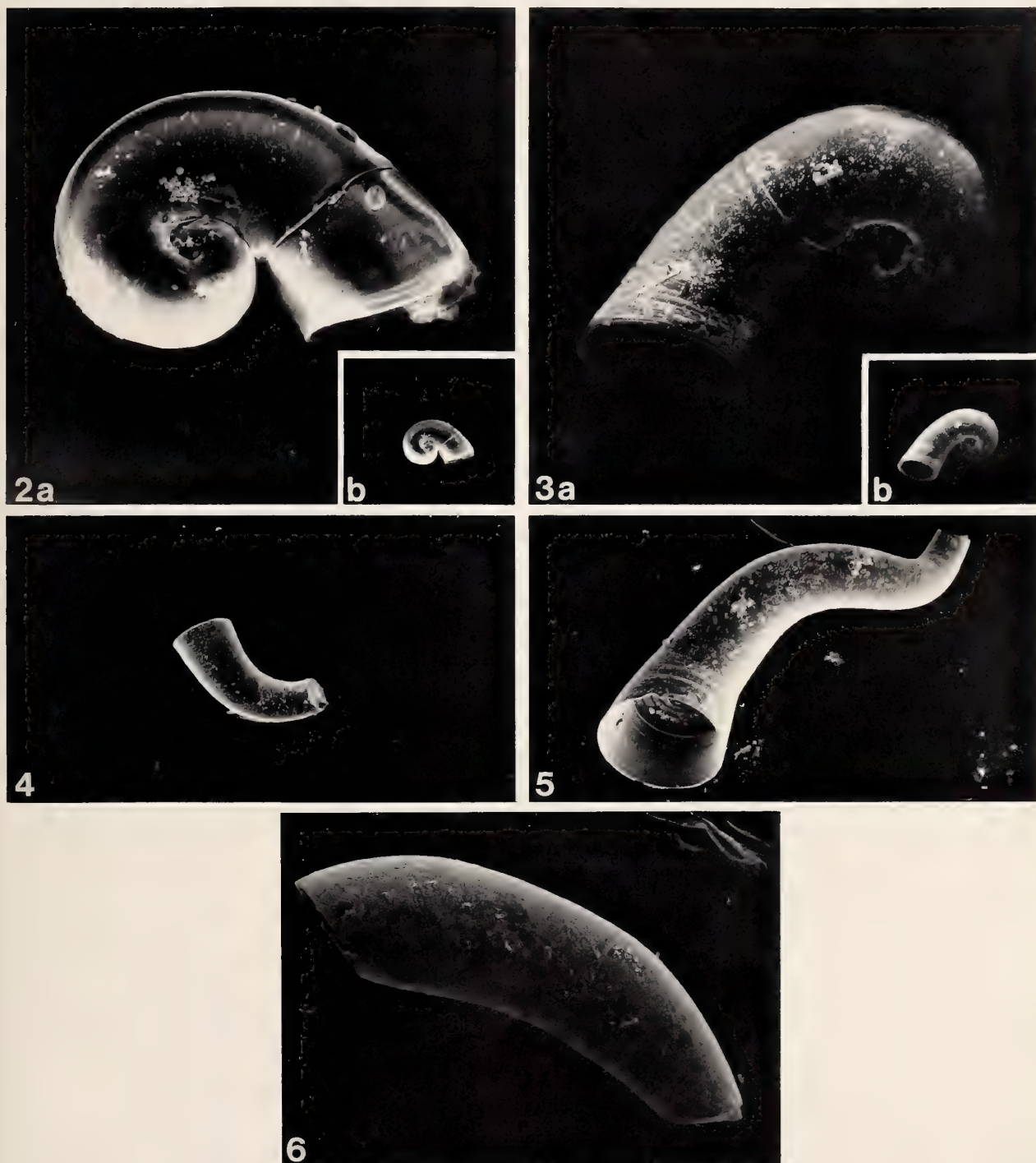
All physical measures were collected between 1000 and 1600 h. Temperature above and within the *Cladophora crystallina* mat ranged between 26 and 27°C. Dissolved oxygen was 8 mg/l in the surface layer of the mat, 5 mg/l in the middle, and less than 3 mg/l (the minimum concentration accurately detectable with the Hach kit) in the bottom layer. The water above the *C. crystallina* mat contained 7 mg/l dissolved oxygen.

Five stages of shell formation were recognized (Figures 2–6). Stage I, the protoconch, exhibits planospiral coiling (Figures 2a, b). Stage II begins when the shell completes roughly a 60° curve to the left, away from the plane containing the planospiral protoconch (Figures 3a, b). After the loss of the protoconch through breakage, individuals were termed Stage III (Figure 4). Stage III shells are curved through at least 60°, and lie in one plane. As growth continues the shell begins to resemble a loosely wound helix. Stage IV shells possess this helical shell (Figure 5) resembling a cornucopia. When the Stage IV posterior curves break off, Stage V is attained (Figure 6). Stage V shells are gently curved, and as with Stages I and III, lie in one plane. Length and aperture diameter in Stage V are up to five times greater than in Stage I. Stage V specimens exhibit polymorphism in that some have parallel rows of white spots on the otherwise amber-brown shell. Animals with white spots were four times more abundant on the surface layer of the alga at all stations (7 individuals without spots, 32 with spots). In the middle of the mat, 37 were plain and 3 were spotted, while in the bottom algal layer neither form was obviously dominant (5 without spots, 4 with spots).

Caecum cornucopiae attains a maximum length of 2.5 mm. The protoconch is white in color, with later stages becoming progressively browner as the shell thickens. The proboscis, head region, and tentacles have variable white areas.

Pearson's product moment correlation coefficient was calculated for the 109 measures of aperture diameter and stage, with a resultant $r = 0.92$. The equation

$$y = 0.11x + 0.02$$



Explanation of Figures 2 to 6

Figures 2-6. Scanning electron micrographs of the stages of shell growth in *Caecum cornucopiae*.

Figure 2a. Stage I, $\times 176$.

Figure 2b. Stage I, $\times 28$.

Figure 3a. Stage II, $\times 119$.

Figure 3b. Stage II, $\times 28$.

Figure 4. Stage III, $\times 28$.

Figure 5. Stage IV, $\times 28$.

Figure 6. Stage V, $\times 28$.



Figure 7

Stage of shell formation vs. aperture diameter for *Caecum cornucopiae*. Bars represent 1 standard deviation around the mean.

where x is shell stage and y represents aperture diameter, may be used to describe this relationship (Figure 7). Because one-way, unequal-N ANOVA's showed each stage class to be significantly different from its adjacent classes ($P \leq 0.01$), all distribution studies of *Caecum cornucopiae* utilized stage instead of aperture diameter as a measure of relative age.

Table 1 presents abundance data from Station 1. Analysis of variance within each layer found the three sites where the top algal layer was sampled to be significantly different from one another ($P = 0.025$), whereas significance was not found in either the middle ($P = 0.683$) or bottom layers ($P = 0.492$).

Abundance of *Caecum cornucopiae* decreased significantly at Station 1 ($P \leq 0.05$) with increasing depth in the algal mat (Table 2). Spirorbid polychaetes, juveniles of the bivalve *Pinctada radiata*, and an unidentifiable juvenile bivalve showed similar zonation. Thickness of the mat of *Cladophora crystallina* varied between 59 and 67 cm at Station 1; there is no evidence this influenced the distribution of *C. cornucopiae*.

One of the 18 replicates collected from the bottom of the algal mat contained 26 *Caecum cornucopiae* whereas the mean of the other 17 replicates was 1.35 animals per sample (standard deviation = 1.32). When standardized

to number per 1 ml of alga, the anomalous replicate contained 16 times more *C. cornucopiae* than the mean of the other 17 replicates. This replicate is not included in Table 2 (** Table 2).

Table 1

Abundance of *Caecum cornucopiae* at Station 1. Three sites ($n = 6$) were sampled at each algal layer. Probability values are presented following ANOVA testing to determine intra-layer variation.

Algal mat layer	Abundance (mean \pm 1 SD)	Probability
Top	266.3 \pm 175.1	0.025
	121.2 \pm 58.9	
	390.6 \pm 172.3	
Middle	67.7 \pm 24.6	0.683
	75.7 \pm 27.3	
	65.0 \pm 8.4	
Bottom	12.2 \pm 9.3	0.492
	26.6 \pm 50.7	
	5.8 \pm 9.7	

Table 2

Abundance data (mean \pm SD) from the surface, middle, and bottom of the *Cladophora crystallina* mat at Station 1. Samples have been standardized to number per 1 ml of alga (displacement volume). * indicates abundances between adjacent layers are significantly different within that species ($P \leq 0.05$) ($n = 18$, except for **, where $n = 17$; see text).

Species	Top layer	Middle layer	Bottom layer
<i>Caecum cornucopiae</i>	252 \pm 175*	70 \pm 23*	8 \pm 8* **
Spirorbid polychaetes	131 \pm 61*	29 \pm 34*	2 \pm 18*
<i>Pinctada radiata</i>	88 \pm 36*	53 \pm 32*	6 \pm 7*
Juvenile bivalve	9 \pm 11*	0.5 \pm 2.0*	0
<i>Leptosynapta</i> sp.	2 \pm 4	0.5 \pm 0.7	0
Ophiuroid	0.5 \pm 1.2	0	0
Flatworm	2 \pm 6	0	0
Anemone	0.3 \pm 1.2	0	0
Nudibranch	0.3 \pm 1.2	0	0
Hydroid	0.3 \pm 1.2	0	0
<i>Polymesoda maritima</i>	0.3 \pm 1.2	0	0.5 \pm 2.4
<i>Eurythoe</i> sp.	0.3 \pm 1.2	0.3 \pm 1.2	0
Larvae	0.3 \pm 1.2	0	0

The stage-frequency distribution at Station 1 also varied with depth within the mat of *Cladophora crystallina* (Figure 8). The percentages of the populations in Stage I at the surface, middle, and bottom of the algal mat were approximately the same. The same trend was seen for

Stage IV. The percentage in Stage II decreased with depth. Stage III animals were most abundant in the bottom algal layer where they were the majority of the population, and were least abundant in the middle of the mat. Animals in Stage V showed a normal distribution with increasing depth in the mat.

The stage-frequency distributions of *Caecum cornucopiae* on the mat surface at Stations 1, 2, and 3 were varied (Figure 9). Station 1 showed a skewed distribution with the population maximum at Stage II. Station 2 seemed to contain a younger *C. cornucopiae* population, with over 70% in Stages I and II. Station 3 showed a more uniform population structure, but with few in Stage I.

A small brachyuran crab, the mottled mojarra *Eucinostomus lefroyi*, and the scrawled cowfish, *Lactophrys quadricornis*, were found to consume *Caecum cornucopiae*. Of the 20 crabs examined, 19 had guts with partially digested food, and all of these contained either shells or opercula of *C. cornucopiae*. The guts of 25 *E. lefroyi* collected during daylight hours were examined; 48% contained *C. cornucopiae* shells (R. Aronson, personal communication). The maximum number of shells in 1 gut was 40, with an average of 5.9; 99.4% of the shells were located in the intestine, suggesting that predation occurred at night. *Caecum cornucopiae* comprised less than 5% of the gut-content volume of one *Lactophrys quadricornis*.

DISCUSSION

The stages of growth herein described were determined by two criteria, loss of previous shell growth and shell shape. It is assumed that loss of previous growth occurs

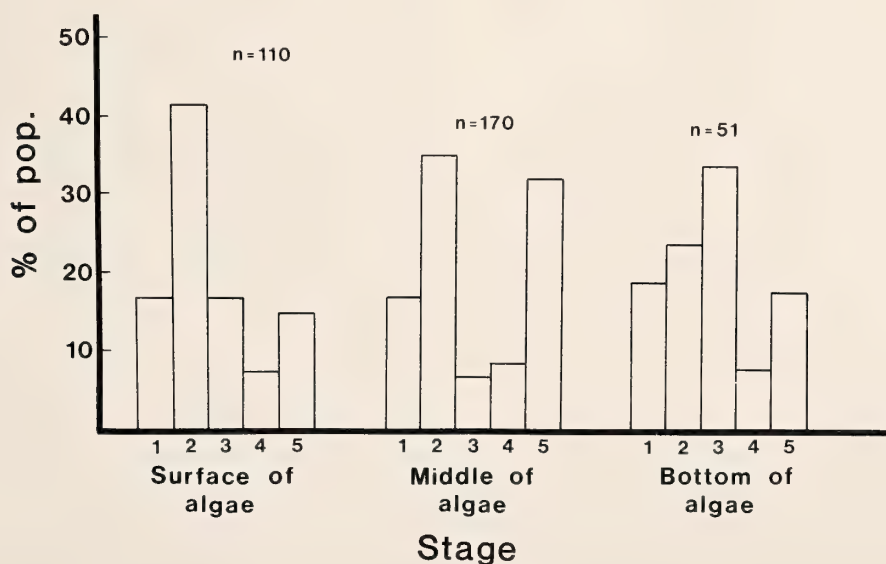


Figure 8

Stage-frequency distribution of *Caecum cornucopiae* from the surface, middle, and bottom layers of the *Cladophora crystallina* mat at Station 1.

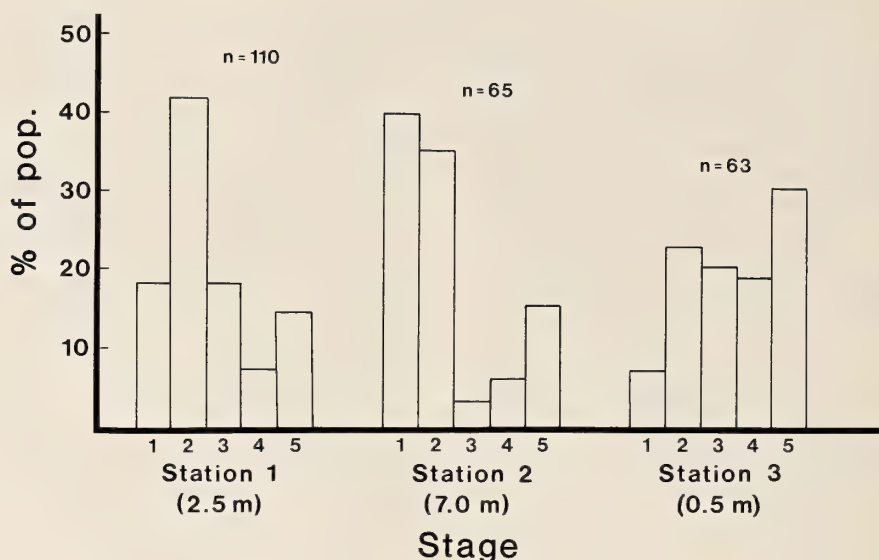


Figure 9

Stage-frequency distribution of *Caecum cornucopiae* in the surface layer of the *Cladophora crystallina* mat at different locations within Sweetings Pond. Water depths are presented below each station designation. Refer to Figure 1 for station locations.

due to breakage. Predatory attempts are not thought to be a primary cause of breakage because it is unlikely that all individuals would experience such attempts. Elements causing breakage in the *Cladophora crystallina* environment have not been recognized.

The ability to utilize aperture diameter as a measure of relative age allowed a great deal of information to be assimilated quickly and accurately. Variation in the range of aperture diameters in each stage was expected because growth is a continuous process (Figure 7).

The pattern of variation in the stage-frequency distribution within the algal mat (Figure 8) is not understood, and may reflect natural variation within the population and/or undocumented movement patterns. Abundance decreased with mat depth, probably as a result of decreased oxygen. However, other potentially limiting factors include the presence of hydrogen sulfide, predation, and food resources, all of which presumably change with algal mat depth.

The distribution of *Caecum cornucopiae* seems patchy. First, analysis of variance of the top algal layer at Station 1 (Table 1) showed the three sites to contain significantly different abundances. Second, the anomalous replicate collected in the bottom layer of the *Cladophora crystallina* mat at Station 1 contained 16 times more *Caecum cornucopiae* than the mean of the other 17 standardized replicates. There are two possible explanations: clumping and sampling error. Sampling error could occur if a piece of *C. crystallina* from the surface layer was carried to the bottom during sampling. However, the other fauna in the sample,

Pinctada radiata and spirorbid polychaetes, were found in densities comparable to the other bottom replicates. It is suggested, therefore, that in this sample the *C. cornucopiae* were clumped around a potentially beneficial resource.

Variation in stage composition with the water depth at which the population was found (Figure 9) suggests two things. First, recruitment may occur earlier in shallow areas. At 7 m, 40% of the population is in Stage I, whereas at 2.5 and 0.5 m, 18% and 8% percent are in Stage I, respectively. Variation in water temperature and/or insolation are possible causes. Second, the stage-frequency distribution representing the population found at 0.5 m suggests decreased post-Stage I mortality as compared to populations at 2.5 and 7 m. Observations revealed the lack of *Eucinostomus lefroyi*, *Lactophrys quadricornis*, and the brachyuran crab, predators of *Caecum cornucopiae*, in shallow water. Such absence might account for the observed distribution.

The presence of Stage V *Caecum cornucopiae* on muslin bags at Station 4 at least 3 m from any *Cladophora crystallina* suggested horizontal movement on or in the sediment. However, the distribution of *C. cornucopiae* in the sediment was not determined.

Five of the six samples reported in Figures 8 and 9 show Stage IV individuals composing less than 10% of the population. Although the cause for this distribution is not known, it may represent a break between reproductive classes, or widespread mortality during development.

The dense population of *Caecum cornucopiae* on mats of *Cladophora crystallina* in Sweetings Pond may have a

significant effect on the alga by consuming epiphytic material or the alga itself. Because of its abundance, *C. cornucopiae* may be an important link in the pond's food web, but only further study will reveal the role that *C. cornucopiae* assumes in this ecosystem.

ACKNOWLEDGMENTS

My thanks to Richard B. Aronson who introduced me to Sweetings Pond and who also collected the *Eucinostomus lefroyi* gut-content data. *Caecum cornucopiae* was identified by T. Abbott, and C. J. Bird identified *Cladophora crystallina*; H. R. Baker, R. D. Burke, L. M. Coon, D. V. Ellis, P. A. Gee, L. A. Taylor, and an anonymous reviewer contributed to the development of the manuscript. This study was supported by National Science Foundation

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The Bermudan and Caribbean Sacoglossan Mollusk *Elysia flava* Verrill Now Recorded from the Greek Aegean Sea

by

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Abstract. This Bermudan type has now been recorded from Tenerife, Jerba (Tunisia), the west coast of the Greek Aegean island of Evia, and the north shore of the Gulf of Corinth. It represents a new record for the Mediterranean Sea and a range-extension of many thousands of kilometers.

INTRODUCTION

ONE OF THE LEAST known sacoglossans (=ascoglossans) of the Atlantic Ocean, *Elysia flava* Verrill, 1901, was first described from the shore at Castle Harbour, Bermuda. It was distinct by virtue of its short, non-papillate rhinophores, white tuberculate parapodial rims, and the white papillae inside the parapodia. VERRILL (1901) studied an unknown number of specimens, up to 18 mm in length; he recorded it as "rare." In 1977 my observations on Jamaican sacoglossans were published, including a description of two specimens of *E. flava*, one from the north of the island, the other from the south (THOMPSON, 1977). These were the first reports of this distinctive species since Verrill's type-description.

Since that time, a further record of *E. flava* has come from ORTEA (1982) who described two specimens, 11 and 13 mm in length, from Tenerife in the Canary Islands; this was the first citation from the eastern Atlantic.

Sublittoral collections in Greek waters in the summer of 1982 have yielded three further specimens, extending the known range by thousands of kilometers. At the same time, Dr. Philippe Bouchet obtained similar material from

the coast near Jerba (sometimes written Djerba), on the Tunisian shores of the Mediterranean Sea. The depth range was 1-8 m. The opportunity was taken to re-investigate the internal anatomy, especially the sexual organs and the radula.

Many other Mediterranean *Elysia* species have been described and illustrated by SCHMEKEL & PORTMANN (1982), and a taxonomic review is being prepared by Dr. Bouchet.

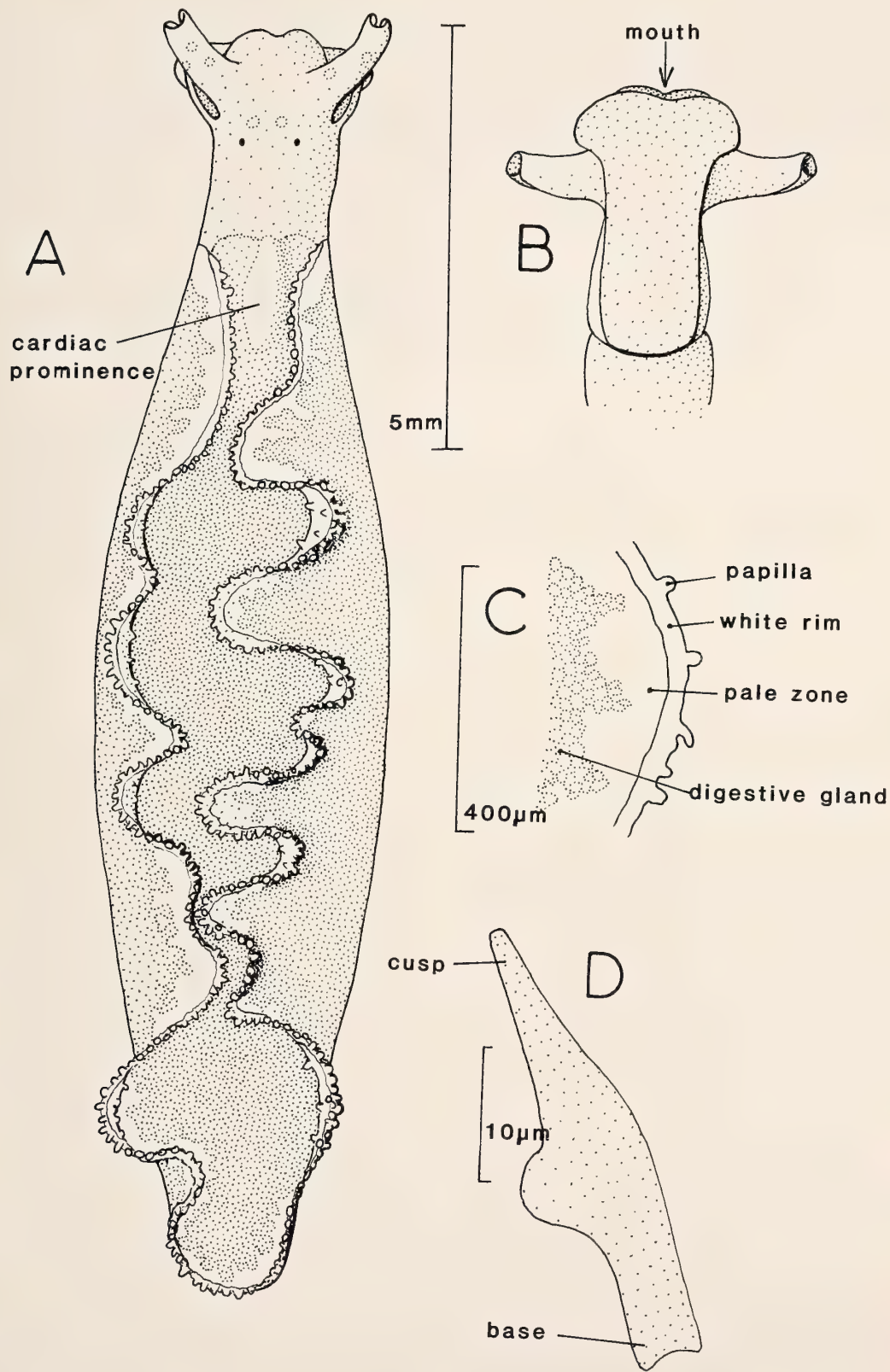
DESCRIPTION

Material. Two specimens were found in subtidal shallows (to 2 m) 4 km to the south of Amarynthos, on the west coast of the Aegean Island of Evia, 23 July 1982 (length 15 mm) and 17 August 1982 (length 10 mm). Another specimen was found in 1 m of water, near Eratini on the north shore of the Gulf of Corinth, 30 July 1982 (11 mm). All were found under loose stones.

External features. The overall color is pale yellowish green, through which the dark green lobes of the digestive gland can be discerned. There is a little crimson speckling

Figure 1

Elysia flava Verrill. A, Dorsal view from life of a 15-mm specimen from Evia, July, 1982. B, Ventral view of the head of the same. C, Enlarged view of the parapodial rim. D, Radular tooth, 34 μ m in length, of a 10-mm specimen from Evia, August, 1982, examined in polyvinyl lactophenol.



on the epidermis of the head, and over much of the rest of the body, both inside and outside the parapodial lobes. The parapodial rim is white and bears numerous blunt papillae; similar papillae can be found inside the parapodia, sparsely distributed. The rhinophores are short and bear a few large white blotches. The head is pale yellow in color, slightly bilobed anteriorly. The propodium is markedly bilobed. There are no gills (blood-engorged folds of the epithelium) inside the parapodia.

Anatomy. The radula of the 10-mm specimen was examined in polyvinyl lactophenol. The formula was $19 \times 0.1.0$; all the teeth were smooth. The 15-mm specimen was serially sectioned. The ovotestis was filled with ripe

eggs and sperm. No spawn was found either in the field or the laboratory.

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Do Oystercatchers Influence Limpet Shell Shape?

by

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Abstract. The Black African Oystercatcher, *Haematopus moquini*, most often attacks limpets at the posterior margin. When feeding on *Patella granularis*, it preferentially attacks individuals that are pear-shaped rather than elliptical, presumably because the posterior margin is more easily distinguished in such shells. *Patella granularis* is more pear-shaped in habitats inaccessible to oystercatchers and in localities lacking oystercatchers, indicating that the selective effect of oystercatchers is sufficient to alter the phenotypic shell shape and probably also the genotypic composition of limpet populations preyed upon.

INTRODUCTION

VARIATIONS IN THE intensity of predation on gastropod populations by fish and invertebrates can lead to regional adaptations in shell morphology (EBLING *et al.*, 1964; VERMEIJ, 1978; PALMER, 1979), but very little is known about predation by birds in relation to shell form (VERMEIJ, 1978; but see HARTWICK, 1981) in spite of the fact that birds may have a substantial impact on limpet populations (FRANK, 1982).

Observations on shell remains lead to the conclusion that African Black Oystercatchers, *Haematopus moquini*, preferentially attack limpets (*Patella* spp.) at the posterior margin of the shell, and make "correct" attack decisions most consistently on limpet species whose posterior and anterior sectors are clearly distinguishable, such as *Patella cochlear* (HOCKEY, 1981). The dominant limpet in the diet of the African Black Oystercatcher is *P. granularis*, an elliptically shaped species of the mid- and upper-intertidal regions of southern Africa (Hockey & Underhill, MS). There is no specific orientation of *P. granularis* on rock faces (unpublished data); therefore, posterior attack is presumed to be choice by the birds. The proportions of attacks delivered by oystercatchers at the posterior, middle, and anterior sectors of the shells of this species are respectively, 49.3%, 12.1%, and 38.6% (n = 487) (HOCKEY, 1981).

Presumably, limpets that are approached from behind by oystercatchers have less warning of the attack and are, therefore, less likely to clamp down prior to attack. If African Black Oystercatchers are most successful when

attacking limpets posteriorly, it would be advantageous, when dealing with a uniformly elliptical species, to attack those individuals which are most pear-shaped, and hence have most recognizable posterior ends. If this strategy is adopted, then two testable hypotheses emerge concerning shell shape within populations of *P. granularis*.

Firstly, limpets in regions where there are no oystercatchers will be more pear-shaped than limpets in regions where oystercatchers occur, where pear-shaped limpets will have been removed preferentially.

Secondly, within regions where oystercatchers occur, limpets in inaccessible sites (vertical rock faces) will be more pear-shaped than accessible limpets, but, assuming genetic control of shell shape, more elliptical than limpets in areas where there are no oystercatchers.

METHODS

Random samples of *P. granularis* were collected at five localities in South Africa and Namibia within the range of the African Black Oystercatcher. Three types of limpets were distinguished: those eaten by oystercatchers (shells collected from chick "middens"); those living on rocks accessible to oystercatchers; and those living on rocks inaccessible to oystercatchers (vertical faces). Oystercatchers do not deposit all the shells that they remove in middens, but chick middens are the most reliable source of large quantities of shells that definitely have been preyed on by oystercatchers. Additionally, collections were made at sev-

Table 1

Mean shell uniformity indexes (SUIs) \pm SD for 17 samples of *Patella granularis* from southern Africa.

Type of limpet population	Sampling location	Mean length (mm) \pm SD	Mean SUI \pm SD
Depredated by oystercatchers	Malgas Is. (33°03'S; 17°55'E)	38 \pm 6	0.91 \pm 0.03
	Possession Is. (27°01'S; 15°12'E)	32 \pm 5	0.92 \pm 0.06
	Jutten Is. (33°05'S; 17°57'E)	45 \pm 11	0.92 \pm 0.04
	Overall mean		0.92 \pm 0.05
Accessible to oystercatchers	Malgas Is.	47 \pm 8	0.95 \pm 0.03
	Owen Is. (29°16'S; 16°52'E)	38 \pm 4	0.94 \pm 0.04
	Jutten Is.	36 \pm 5	0.93 \pm 0.03
	Cape Columbine (32°50'S; 17°50'E)	27 \pm 3	0.94 \pm 0.04
	Overall mean		0.94 \pm 0.04
Inaccessible to oystercatchers	Malgas Is.	36 \pm 5	0.92 \pm 0.04
	Jutten Is.	31 \pm 4	0.91 \pm 0.04
	Cape Columbine	24 \pm 3	0.93 \pm 0.06
	Overall mean		0.92 \pm 0.04
Predator-free	Swakop River (22°41'S; 14°31'E)	30 \pm 6	0.86 \pm 0.08
	Mile 105 (21°25'S; 13°50'E)	50 \pm 6	0.87 \pm 0.04
	Terrace Bay (20°00'S; 13°00'E)	31 \pm 6	0.93 \pm 0.03
	Mowe Bay (19°20'S; 12°43'E)	37 \pm 6	0.90 \pm 0.05
	Rocky Point (19°01'S; 12°29'E)	34 \pm 6	0.92 \pm 0.04
	Angra Fria (18°20'S; 11°58'E)	29 \pm 6	0.86 \pm 0.09
	Kunene River (17°20'S; 11°50'E)	50 \pm 7	0.88 \pm 0.07
	Overall mean		0.89 \pm 0.06

en sites in northern Namibia which are free from oystercatcher predation. Each sample comprised 30 individuals of various sizes, but the limpets selected for measurement fell within the size range eaten by oystercatchers (Hockey & Underhill, MS). All samples were taken from shores with high wave action.

For each limpet, a Shell Uniformity Index (SUI) was calculated. The SUI was the ratio of the width of the shell one third of the way from the anterior edge to the width one third of the way from the posterior edge: thus, individuals with SUIs close to unity were more elliptical than those with lower SUIs. Shell widths were measured with vernier calipers to the nearest 0.5 mm. For each sample a mean \pm SD was calculated, and mean SUIs were compared between samples using a t-test. Data (SUIs) were normalized using an arc sin transformation ($Y' = \sin^{-1}(\sqrt{Y})$) to allow statistical comparison. Limpet length (maximum, in mm) also was measured.

To test whether SUI is influenced by wave action independently of predation, two samples of 30 inaccessible limpets were collected at Froggy Pond (34°12'S; 18°28'E). One sample was taken from an area exposed to heavy wave action and the other from a sheltered area. These two samples contained a wide range of sizes and also were used to test whether SUI is related to size.

RESULTS

Shell Uniformity Indexes ranged from 0.86 ± 0.04 to 0.95 ± 0.03 (Table 1). T-tests indicated the following differences between populations of limpets in different regions and sites.

(a) The mean SUI for all limpets in predator-free populations (0.89 ± 0.06 , $n = 210$) was significantly less ($t = 6.89$, $P < 0.001$) than for limpets from all depredated populations (0.93 ± 0.04 , $n = 300$).

(b) Inaccessible limpets had a significantly lower SUI than accessible limpets at Malgas Island ($t = 3.16$, $P < 0.01$) and at Jutten Island ($t = 2.27$, $P < 0.05$), both islands with high densities of oystercatchers (respectively 60 and 63 birds per km of shore). Inaccessible limpets were not significantly different from accessible limpets at Cape Columbine ($t = 1.07$, $P > 0.1$), an area with lower oystercatcher density (two birds per km), although the trend was in the same direction. Overall, inaccessible limpets had a significantly lower SUI than accessible limpets ($t = 2.93$, $P < 0.01$).

(c) Limpets taken by oystercatchers had a significantly lower SUI than accessible limpets at Malgas Island ($t = 4.64$, $P < 0.001$), but at Jutten Island the difference was not significant ($t = 0.25$, $P > 0.1$) although the trend was

in the same direction. Densities of oystercatchers at the two sites are similarly high, but at Malgas Island, the proportion of *P. granularis* in the diet (36%) is greater than at Jutten Island (26%) (Hockey & Underhill, MS). Overall, limpets taken by oystercatchers had a lower SUI than all accessible limpets ($t = 3.49$, $P < 0.001$).

(d) Inaccessible limpets in depredated populations overall had a greater SUI than limpets in predator-free populations ($t = 2.32$, $P < 0.05$).

Patella granularis grows allometrically, shell height increasing faster than shell length (BRANCH, 1975), but SUI was not correlated with limpet size (Table 1), in predator-free populations ($r = 0.17$, $P > 0.1$), in all samples combined ($r = 0.45$, $P > 0.05$) or in the additional samples from Froggy Pond ($r = 0.12$, $P > 0.2$), so that variation in limpet size can be eliminated as a factor influencing SUIs. Similarly, wave action does not influence SUI. In both samples from Froggy Pond (one sheltered, one exposed) the mean SUI was 0.94 ± 0.03 .

DISCUSSION

The hypothesis that limpets in predator-free populations will be more pear-shaped than those in depredated populations was upheld. Similarly, the hypothesis that accessible limpets will be more elliptical than inaccessible limpets was supported in areas where the density of oystercatchers is high. At a low density site, Cape Columbine, the trend was the same but not significant.

The mean SUIs for inaccessible limpets and limpets consumed by oystercatchers were the same, but the former was significantly higher (*i.e.*, shells more elliptical) than the mean SUI for predator-free populations. This further supports the second hypothesis and implies that shell shape is, at least to some extent, genetically determined, and that predation by oystercatchers influences the limpet gene pool. If this were not the case, inaccessible and predator-free populations would have similar SUIs.

The possibility of a latitudinal influence on shell shape was considered, but Table 1 clearly illustrates that there is no trend in shape with decreasing latitude.

There are no other important vertebrate predators of *P. granularis*. Very small individuals are occasionally taken from mussel beds by Turnstones, *Arenaria interpres*, and Whitefronted Plovers, *Charadrius marginatus*; and the Giant Clingfish, *Chorisochismus dentex*, preys on limpets;

but *P. granularis* is a negligible component of the diets of these three species (STOBBS, 1980; BRANCH, 1981; personal observations).

From this we conclude that the selective influence by oystercatchers alone on the genotypes of *P. granularis* is sufficient to be detectable in the phenotypes.

ACKNOWLEDGMENTS

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NOTES, INFORMATION & NEWS

A Range Extension of *Nassarius miser* (Dall, 1908)

by

Robert T. Howley
11760 Gilmore Street,
North Hollywood, California 91606

On October 2, 1982, an otter trawl was brought up from a black mud bottom at a depth of 250 fathoms off Resort Point, Palos Verdes Peninsula, Los Angeles County, California. Contents included the gastropods *Acteocina eximia* (Baird, 1863), *Amphissa bicolor* (Dall, 1892), *Bittium* sp., *Mitrella permodesta* (Dall, 1890), *Nassarius insculptus* (Carpenter, 1864) and a species of *Nassarius* represented by five specimens. Those five shells were identified by Dr. James McLean, Los Angeles County Museum of Natural History, as *Nassarius miser* (Dall, 1908). One is deposited at this museum and the others remain in the author's collection.

The northern range of *Nassarius miser* is cited as Cedros Island, Baja California, Mexico, in A. M. KEEN (1971, *Sea Shells of Tropical West America*, Stanford University Press). The most northern part of Cedros Island is approximately 28°22'N latitude, 115°11'W longitude. Resort Point is approximately 33°50'N latitude, 118°25'W longitude. This is a range extension north of over 500 km and, I believe, is the first published record of *N. miser* from California.

I thank Ed Tarvyd, professor at Santa Monica City College, through whose courtesy I was on board the research vessel Vantuna. I also thank Dr. McLean, as well as the captain and crew of the Vantuna.

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scientific quarterly, *The Veliger*. Donations to the Society are used to pay a part of the production costs and thus to keep the subscription rate at a minimum. Donors may designate the Fund to which their contribution is to be credited: Operating Fund (available for current production); Savings Fund (available only for specified purposes, such as publication of especially long and significant papers); Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

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Donations in Memory of Lucinda Draper

Mrs. Lucinda V. Draper, a native of Iowa, passed away suddenly on June 26. She was the wife of Bertram C. Draper, and both have been long-time members of the Conchological Club of California. A Memorial Fund has been set up honoring Mrs. Draper, and in accordance with the wishes of Mr. Draper, the proceeds have been sent to the Veliger Endowment Fund. Donors include the following: Mrs. Edith Abbott, Mrs. Jean Cate, the Conchological Club of Southern California, Mrs. Helen DuShane, Mr. Joseph DuShane, Dr. James McLean and Ms. Jo-Carol Ramsaran.

The California Malacozoological Society acknowledges these generous donations with gratitude, and extends its sympathy to Mr. Draper.

BOOKS, PERIODICALS & PAMPHLETS

Marine Animals of Baja California A Guide to the Common Fish and Invertebrates

by DANIEL W. GOTSHALL. 1982. Sea Challengers: Los Osos, California. 112 pp.; 213 color photographs. \$17.95 paperback; \$29.95 hard cover.

This field guide, designed to be used primarily by sport divers and naturalists, provides photographs and brief commentaries on 125 species of fishes and 62 species of invertebrates encountered in the shallow waters surrounding the Baja California peninsula. For each photograph, common and scientific names are listed along with habitat, geographic range, maximum known size, and one or two identifying characters.

The book's primary flaws, many small sins of omission in species coverage and identification, are mostly intentional or at least understandable. Excluded are most of the fishes and invertebrates whose southern range extends down the outer coast of Baja from California (these are covered in other books by the author). Also excluded are small, difficult-to-identify animals and those to be found only by digging or turning over rocks. Our readers particularly may regret the decision to include few mollusks (the rationale is that mollusks are well covered in other books)—only nine species of mollusks are illustrated compared, for example, with 20 species of cnidarians. Also worth noting is the fact that 14 of the 62 species of invertebrates included are identified no further than to genus, a result of limited taxonomic study in the area and the author's understandable reluctance to "guess" at identifications from photographs.

Despite these limitations, this book is a useful and thoroughly enjoyable contribution. It is apparently the first all-color photographic guide to both the fishes and invertebrates of Baja California. The photographs are exceptionally fine, vivid and informative, and they are printed with obvious care and craftsmanship. Both the author and the publisher are to be complimented for the superb quality of the plates. In short, this book clearly belongs in the luggage of anyone planning to visit the marine animals of Baja California, just as it belongs on the shelves of armchair naturalists who enjoy simply gazing at the beauty of marine life.

D. W. Phillips

Tertiary Marine Pelecypods of California and Baja California: Nuculidae Through Malleidae

by ELLEN JAMES MOORE. 1983. U.S. Geological Survey

Professional Paper 1228-A, 108 pp., 27 pls., 2 figs., 8 tables.

In this, the first chapter of a projected compilation of all Californian Tertiary marine mollusks, 233 species of the Nuculidae, Malletiidae, Nuculanidae, Solemyidae, Arcidae, Parallelodontidae, Cucullaeidae, Noetiidae, Limnopsidae, Glycymerididae, Manzanellidae, Mytilidae, Pinnidae, Pteriidae, Isognomonidae, Pulvinitidae, and Malleidae are illustrated, their original descriptions quoted, comparisons made to other species, geographic and stratigraphic range cited, depth range and habitat described when known or inferred with confidence, and modern taxonomic assignments made. The result is a supremely useful synthesis, sure to realize its goal of improving the utility of marine mollusks in Cenozoic biostratigraphy of the northeastern Pacific.

The work will also be a significant reference for Alaskan, northwestern Pacific, and Neotropical faunas, all of which share genera and species with the Californian realm. Of 52 genera of the included families that now occur in the eastern Pacific region (Bering Strait to Cape Horn; BERNARD, 1983, Canadian Spec. Publ. Fisheries & Aquat. Sci. 61), 32 (62%) have a Tertiary fossil record in California or Baja California. Neontologists ignore this at their peril.

Type localities, location of type material, and synonyms are given; where possible, the illustrations are of type specimens. For large families, distribution tables show graphically the geographic and geologic distribution of eastern Pacific species from Alaska to Central and/or South America. Occurrence in the Californias is listed by formation; a table gives series-epoch assignments for all formations cited.

Even a compilatory work like this one contains some subjective judgments—particularly on taxonomic matters—hence, room for debate. For example, it will be interesting to see whether *Adula? mcknighti* (Hanna, 1927) ultimately proves to be an *Adula* or perhaps, with its coiled, nearly terminal beaks, a species of *Botula*. I doubt whether *Perna montana* Conrad, 1857, is properly assigned to the mytilid genus *Perna* Retzius, 1788, rather than the isognomonid *Perna* Bruguière, 1789, which Conrad seems to have had in mind.

All debater's points aside, the "Moore Synthesis" will be a paleontologists' companion and standard volume for years to come. I hope that the Geological Survey will give high priority to the production and publication of future chapters.

B. Roth

**Morphologie und Bildung der frühontogenetischen
Gehäuse bei conchiferen Mollusken**
(Morphology and formation of the early ontogenetic
shells of conchiferan mollusks)

by KLAUS BANDEL. 1982. Facies 7:1-198, pls. 1-22, 109 text figs., 6 tables, Erlangen. (In German with English summaries in the text.)

This is a must for every student not only of early ontogenetic shells, but of the entire molluscan ontogeny and phylogeny. The work starts with detailed personal observations on selected species of archeogastropods *sensu stricto*, neritaceans, mesogastropods, neogastropods, ammonites, and recent cephalopods (*Sepia*, *Spirula*, *Nautilus*), to lead the reader into a discussion on successively more comprehensive aspects of the ontogeny, phylogeny, and classification of the phylum Mollusca.

Highlights are:

- in archeogastropod ontogeny, the presentation of a course of events different from most textbooks, which, if confirmed and generalized, must mean that the Garstang-Crofts model of archeogastropod torsion is now out;
- a rejection of the idea that Fissurellidae gave rise to Scissurellidae by means of neoteny;
- discovery of shell pores in *Puncturella* and *Emarginula*, but not in *Fissurella*;
- further evidence that Neritacea show little similarity to the rest of the archeogastropods, but are related to the mesogastropods;
- examples of variations in ontogeny of higher gastropods, which suggest that ecological and functional pressures frequently changed the course of gastropod ontogeny;
- precisions and corrections to previous studies on the earliest ontogeny of ammonite shells and comparison with shells of living cephalopods; a modification of the model of monoplacophoran or early gastropod origin of cephalopods;

- a discussion of the characters of monoplacophorans; the question of primary versus secondary metamery cannot be solved with the present knowledge of this class, a circumstance aggravated by the shortcomings of the fossil record: beyond the insufficient state of preservation, there is the ambiguity of properties such as the position of the apex, the bilateral symmetry of the shell, and apparently metameric muscle impressions, which may be found in similar appearance in limpet-like gastropods as well; in many fossils not even the distinction between monoplacophorans and gastropods is proven.
- many critical comments on the taxonomic significance of various properties are interspersed in the text: for example, of archeogastropod primary shell sculpture; of the slit and its derivatives; of characters of limpet-like shells such as secondary mineral deposits (callus) in the apex, loss of the primary shell (the "protoconch"), and development of secondary bilateral symmetry; of the shape and size of the inner protoconch of cephalopods; and of the presence of shell pores.

To the taxonomist one impression remains: many features, from the muscle-scars of limpet-like shells, to the cephalopodan inner protoconch, and to the bilateral symmetry, seem to be determined by function and physiology, and, thus, might have been developed repeatedly, rather than indicating the common origin of their bearers. Some soul-searching needs to commence, especially among those concerned with paleozoic mollusks and with the classification of the larger taxonomic units.

The author has combined a plethora of observations of his own with vigorous literature digestion. Having himself brought down a few theories might have cautioned him not to create too many new ones, except for his model of archeogastropod torsion. Regardless, this work provides in every chapter food for thought and stimuli for further research. By reading this book, one can relive the fascination exerted by the observation of growth, construction, and final form that carried the author through his studies.

D. Kadolsky

Manuscripts

Manuscripts must be typed on white paper, 8½" by 11", and double-spaced throughout (including references, figure legends, footnotes, and tables). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (SMITH, 1951), for two authors (SMITH & JONES, 1952), and for more than two (SMITH *et al.*, 1953).

The "literature cited" section must include all (but not additional) references quoted in the text. References should be listed in alphabetical order and typed on sheets separate from the text. Each citation must be complete and in the following form:

a) Periodicals

CATE, J. M. 1962. On the identification of five Pacific *Mitra*. *The Veliger* 4:132-134.

b) Books

YONGE, C. M. & T. E. THOMPSON. 1976. *Living marine molluscs*. Collins, London. 288 pp.

c) Composite works

FEDER, H. M. 1980. Asteroidea: the sea stars. *In*: R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal invertebrates of California*. Stanford Univ. Press, Stanford, Calif. pp. 117-135.

Tables

Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend.

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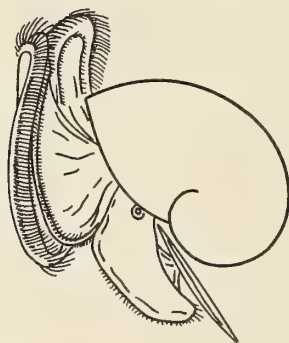
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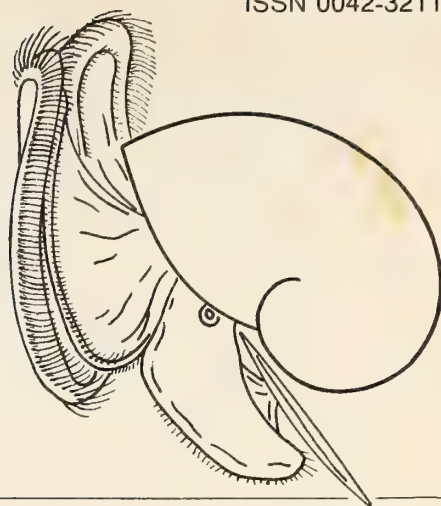
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This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater, or terrestrial mollusks from any region will be considered. Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimen must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Very short papers, generally not exceeding 500 words, will be published in a column entitled "NOTES, INFORMATION & NEWS"; in this column will also appear notices of meetings, as well as news items that are deemed of interest to our subscribers in general.

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Activity, Dispersion, and Size of *Lanistes nyassanus* and *L. solidus* (Gastropoda, Ampullariidae) over the Depth Gradient at Cape Maclear, Lake Malawi, Africa

by

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Abstract. We examined the hypothesis that a diel cycle of activity accounts for daily variation in observed density of two endemic, lacustrine species of *Lanistes*: *L. nyassanus* and *L. solidus*. Snail activity, density, and size were recorded over the 1.5–35.5 m portion of the water depth gradient at Cape Maclear, Malawi, in the southern part of Lake Malawi, during both cool-wet (1980, 1981) and warm-dry seasons (1981, 1982). Population parameters were quantified. A diel cycle of activity occurred for both species of *Lanistes* at all depths in both seasons. The population activity patterns and dynamics of these related species are hypothesized to: (1) be independent of each other but correlated with micro-habitat structure; and (2) reflect food availability in one case (*L. solidus*) as well as a refuge from cichlid predation for recruits of both species.

INTRODUCTION

THE ENDEMIC prosobranch mollusks of Lake Malawi, Africa, form a complex, relatively speciose group; as such they represent a model of the more extensive gastropod radiation observed in tropical deep lakes compared to temperate ones (BOSS, 1978; HUTCHINSON, in press). Yet, few data exist on the activity, dynamics, or interactions of any of these assemblages (LIVINGSTONE, 1981, p. 179). Two particular aspects formed the focus of our study of the population dynamics of the apple snails (Ampullariidae) at Cape Maclear, Lake Malawi: activity patterns and population distribution patterns along the environmental depth gradient.

Activity patterns are characteristic for species and significant for the dynamics and interactions of populations in communities (ORIANI & SOLBRIG, 1977). Cycles in activity can influence apparent density (LOUDA & MCKAYE, 1982), resource utilization (ORIANI & SOLBRIG, 1977), and vulnerability to predation (PHILLIPS, 1977; WELLS, 1980). Furthermore, predation by fishes has been hypothesized to be a significant selective pressure on aquatic gas-

tropods in general (PHILLIPS, 1977; VERMEIJ & COVICH, 1978; WELLS, 1980) and on two Lake Malawi species in particular (WRIGHT *et al.*, 1967; LOUDA & MCKAYE, 1982). Offset diel patterns of activity seem to be an important aspect of the fish-snail interaction in Lake Malawi. The molluscivorous cichlid fishes are diurnal (McKaye, unpublished data; Louda, personal observation) whereas the gastropods are nocturnal (LOUDA & MCKAYE, 1982; Louda, unpublished data). A diel pattern of movement, along with partial burrowing, which has been documented for marked snails in shallow (1–3 m) water (LOUDA & MCKAYE, 1982), accounts for anecdotal observations of variation in density (GRAY, 1980) of *Lanistes nyassanus* Dohrn, 1865, over a daily cycle.

In the work described here we examine the consistency of the diel activity pattern of *L. nyassanus*: (1) at a range of depths (1–34 m), (2) in different seasons (cool-dry *versus* warm-wet), and (3) in relation to that of a co-occurring species (*L. solidus* Smith, 1877). Additionally, we quantify population density, dispersion, and size distributions along the depth contour for both species.

Three major questions are asked. First, does a diel activity pattern occur for both species of *Lanistes* and is the pattern consistent among depths? Second, what are the population parameters with depth and is there any evi-

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dence of competitive interaction between congeners, species that would be predicted to have similar ecological requirements? Third, is snail distribution related to predation and microhabitat?

STUDY SYSTEM

Our observations were made along a 4-km section of sandy beach adjacent to the Fisheries Research Station at Cape Maclear (34°50'E; 14°5'S), in the southern region of Lake Malawi, 12 km west of Monkey Bay, Malawi (see LOUDA & MCKAYE, 1982, fig. 1). This section of beach has high densities of both *Lanistes nyassanus* and *L. solidus* in shallow water (GRAY, 1980; LOUDA & MCKAYE, 1982); they coexist there with about 16 species of smaller gastropods (LOUDA *et al.*, 1983). There is an annual cycle in water temperature; it is highest (29°C) in the warm, wet season of January–April and lowest (21°C) in the cool, dry season of June–August (MCKAYE, 1983).

The Ampullariidae (=Pilidae) are medium to large (total length ≤ 10 cm), globose snails characterized by a taenioglossate radula and a concentric operculum (WORLD HEALTH ORGANIZATION, 1977; BROWN, 1980). The two species of *Lanistes* are endemic to Lake Malawi and coexist in the shallow portion of the shore around Cape Maclear. *Lanistes nyassanus* is distinctive, being more depressed (BROWN, 1980, fig. 28) and usually larger and heavier than other species of *Lanistes*. However, *L. solidus* is similar to *L. ellipticus* Martens, 1866, which occurs primarily on marsh vegetation around the lake (CROWLEY *et al.*, 1964; CANTRELL, 1979). In fact, *L. solidus* may be a heavier lacustrine form of *L. ellipticus* (BROWN, 1980, and personal communication).

METHODS

Our observations of *Lanistes* species were made using SCUBA during four periods: 18 June–30 August 1980, 17 February–20 March 1981, 7 August–1 September 1981, and 9–23 February 1982. June–August is the cool, dry season; February–March is in the warm, rainy season at this latitude.

The following data were collected by divers visually searching 12.5 \times 2-m transects placed along specified depth contours: (1) number of *L. nyassanus* and *L. solidus*, (2) activity, and (3) aperture length of all *Lanistes* encountered. The high (96%) efficiency of visual search using SCUBA over the open sand habitat was verified by (a) direct search (hand raking) of the top 5 cm of substrate ($N = 100$ m²), (b) quadrat collection (LOUDA *et al.*, 1983), and (c) the consistency of visual density observations in the morning and afternoon on a permanent 128 m² grid (LOUDA & MCKAYE, 1982; LOUDA, unpublished data). Inter-observer agreement also was verified (Kruskal-Wallis Test, $P > 0.10$). All data were collected at 12 3.0-m depth intervals from 1.5–35.5 m.

Snail activity was scored as (1) more than one-half bur-

ied in the substrate or (2) less than one-half buried or active on the substrate surface. During the first two observation periods we also recorded whether or not active snails were in a semi-inverted posture with foot extended into the current. This behavior, presumably feeding (described in LOUDA & MCKAYE, 1982), is of special interest. Although filter feeding is known among ampullariids (JOHNSON, 1952; CHEESMAN, 1956; McCLARY, 1964), it is relatively uncommon among gastropods and is not the usual, rasping mode of feeding of most Ampullariidae (YONGE, 1938).

Aperture length was used as an estimate of size because it represents body size, varies less than other measures as shell wear occurs (FOTHERINGHAM, 1971; LOUDA, 1979), and correlates well with total shell length for *L. nyassanus* (LOUDA & MCKAYE, 1982).

RESULTS

Activity

Afternoon activity always exceeded morning activity for both species. A significantly higher proportion of individuals were active on the substrate surface between 1500 and 1800 h than between 0500 and 0800 h at all depths (Figure 1) in both seasons (Table 1). Occurrence of the inverted posture among all snails observed did not vary with time of day; however, occurrence was higher in the cool season than in the warm season for both species (Table 2). Among active snails of both species, the proportion in the inverted posture, and presumed to be feeding (LOUDA & MCKAYE, 1982), was significantly greater in the morning than in the afternoon; also, among the active *L. solidus* there was a significant decrease in this type of activity during the warm season compared to that in the cool season (Table 2).

Density

Four main points stand out in the data. First, the density of both species was greatest in shallow water. The highest densities of *Lanistes nyassanus* (18.3/25 m²) were observed at a depth of 1.5 m (Table 3A) and those of *L. solidus* (72.0/25 m²) at a depth of 4.6 m (Table 3B). Density of *L. nyassanus* over the rest of the gradient below 10.8 m remained relatively constant (4–8/25 m²). Density of *L. solidus*, however, dropped sharply to less than 1/25 m² below 4.6 m (Table 3B). No live specimens of *L. solidus* have been observed by us below 22 m in the Cape Maclear region of southern Lake Malawi.

Second, until 1982 the densities of *L. solidus* were generally much higher than those of *L. nyassanus* in the shallow area in which they overlap. The density of *L. solidus* at 4.6 m was four to eight times higher than the density of *L. nyassanus* for all paired 1980 and 1981 observations. The density of *L. solidus* at 1.5 m also was greater for the last three out of the four dates (Table 3).

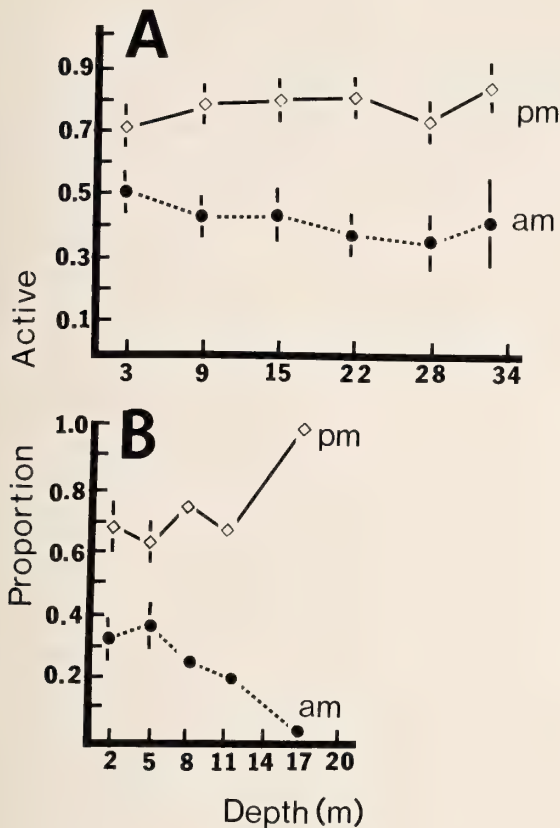


Figure 1

Average proportion active between 0500 and 0800 h (●---●) and between 1500 and 1800 h (◇---◇), both seasons combined, along the depth gradient at Cape Maclear ($\bar{X} \pm 95\%$ confidence limits; statistics on arcsine-transformed data). A. *Lanistes nyassanus* ($N \geq 305, 183, 153, 183, 136$ and 50 at depths to 32 m, respectively). B. *Lanistes solidus* ($N \geq 255, 394, 4, 2$ and 1 at depths to 17 m, respectively).

Third, the distribution of *L. nyassanus* tended to change over the depth gradient between seasons. The highest density of *L. nyassanus* was deeper in each cool, dry season than it was in the succeeding warm, wet season (Table 3A). During the 1980 cool season, density of *L. nyassanus* was highest at 4.6 m. In the succeeding warm season of February–March 1981, *L. nyassanus* density increased significantly at 1.5 m and decreased at three greater, adjacent depths (Table 3A). In the second cool, dry season (1981) *L. nyassanus* numbers dropped sharply in the shallow depths (1.5 – 7.7 m) while increasing significantly at 10.8 m (Table 3A). Increases at one depth were accompanied by decreases at other depths for *L. nyassanus*; thus, distribution, rather than absolute number, must have changed between seasons. Finally, in the second warm, wet season the highest densities were again at shallower depths (4.6 and 1.5 m); however, all densities were lower,

Table 1

Activity of *Lanistes* species by season (cool, dry = June–August 1980 and 1981; warm, wet = February–March 1981 and 1982).

Species Season Parameter	Morning (0500– 0800 h)	Afternoon (1500– 1800 h)	Total
<i>L. nyassanus</i>			
Cool, dry			
N	864	890	1754
Proportion active	0.434	0.804	0.622
95% C.I.	0.39–0.47	0.76–0.84	0.59–0.64
Warm, wet			
N	524	540	1064
Proportion active	0.391	0.592	0.493
95% C.I.	0.34–0.43	0.55–0.62	0.46–0.52
<i>L. solidus</i>			
Cool, dry			
N	540	660	1200
Proportion active	0.293	0.686	0.509
95% C.I.	0.24–0.34	0.64–0.73	0.49–0.53
Warm, wet			
N	438	412	850
Proportion active	0.311	0.568	0.435
95% C.I.	0.27–0.33	0.52–0.62	0.38–0.47

suggesting a decline in absolute numbers as well as a shift in distribution.

Fourth, the density of *L. solidus* dropped over the 20 month period (Table 3B). Density of *L. solidus* remained highest at the 4.6 -m depth in all seasons, but total numbers dropped markedly in each subsequent season after the first year (Table 3B). This decrease in *L. solidus* density at 4.6 m was not accompanied by increases in density at other depths except in the warm wet season of 1981 (Table 3B); thus, emigration or mortality occurred for *L. solidus* over the year between the warm wet season of 1981 and that of 1982.

Size Distribution

The average size of individuals generally increased as depth increased. Initially for *L. nyassanus*, average aperture length was lowest (3.0 cm) at 4.6 m and increased (to 3.6 cm) at 29.4 -m depth (Table 4A). The trend of increased size of *L. nyassanus* with increased depth was consistent for all seasons. The exception was the equal, or greater, average size at the shallowest depth (1.5 m) compared to those at the next, adjacent (4.6 m) depth in all four samples (Table 4A). Interestingly, individuals of *L. nyassanus* were significantly larger in the warm seasons than in the cool seasons (Table 4A). *Lanistes solidus* averaged 2.4 cm (SE 0.03); but, in contrast, these snails were consistently smaller in the warm wet season than in the cool, dry (Table 4B). Size was generally lower in 1981 at

Table 2

Occurrence of inverted posture for species of *Lanistes* at Cape Maclear by season (cool, dry season 1980; warm, wet season 1981) and by time of day (AM = 0500-0800 h; PM = 1500-1800 h). * = $P \leq 0.05$; ** = $P \leq 0.01$.

Species	Total observed	Number active	Number inverted	Inverted among total		Inverted among active	
				%	χ^2_1	%	χ^2_1
<i>L. nyassanus</i>							
Time							
AM	739	315	50	6.8	0.09	15.9	7.11**
PM	726	535	52	7.2		9.7	
Season							
Warm, wet	505	266	26	5.1	3.95*	9.8	1.80
Cool, dry	960	584	76	7.9		13.0	
<i>L. solidus</i>							
Time							
AM	551	197	24	4.4	2.14	12.2	13.78**
PM	675	447	19	2.8		4.3	
Season							
Warm, wet	592	238	8	1.4	14.45**	3.4	6.67**
Cool, dry	634	406	36	5.5		8.6	

4.6 m, i.e., where over 95% of the individuals occurred (Table 3B). Furthermore, the few individuals found at deeper depths, below 4.6 m, were large ($N = 22$, $\bar{X} = 2.7$ cm, $SE = 0.09$) for the population (Table 4B), in a pattern similar to that of *L. nyassanus*.

Three main facts are evident from the size-frequency data. First, no significant differences related to season were observed in size-frequency distributions for either species (Figure 2). Second, the modal (3.3-3.4 cm) and mean (3.2-3.5 cm) sizes for *L. nyassanus* for each season were higher than those for *L. solidus* (mode = 2.3 cm, mean = 2.3-2.4 cm) (Figure 2). Third, no small, young specimens of either species, those with an aperture less than 1.0 cm, were observed on the transects in either warm or cool seasons. Because small individuals (<1.0 cm total length) are extremely rare but after extensive searching have been found among the vascular macrophyte stems at 3-5 m in the study region (LOUDA & MCKAYE, 1982), the data here support the suggestion that the occurrence and recruitment of small individuals of *Lanistes* is patchy, extremely restricted, and related to microhabitat heterogeneity.

DISCUSSION

Casual observations suggested lower densities of *Lanistes* species in the mornings than in the afternoons at Cape Maclear (GRAY, 1980). However, by following marked snails in shallow water, LOUDA & MCKAYE (1982) found that actual, visually-recorded quantitative densities did not change; instead, partial burial of *L. nyassanus* via diel movement into and out of the sand substrate occurred, giving the superficial impression of changing density. The present study extends the available observations over the environmental gradient. We found that a diel pattern of

activity occurred for both species, at all depths, and in both seasons (Figure 1, Table 1).

The three main hypotheses to explain the adaptive value of a diel pattern are: (1) physiological limits to activity, (2) intrinsic (canalized) gastropod behavior, and (3) predator avoidance. Further work is required to separate these hypotheses. Our observations, however, suggest physiological limits to diel activity are unlikely. Although overall activity appeared lower during the warm season (Table 1), it was high under all conditions.

Predation pressure was intense, reinforcing any intrinsic tendency toward nocturnal activity. The predators on gastropods, such as birds (e.g., ZACH, 1978), crabs (VERMEIJ & COVICH, 1978), or fishes (FRYER & ILES, 1972; MCKAYE, personal observation), are diurnal, visual hunters. Effective diurnal predators should exert strong selective pressure for nocturnal activity on their prey. Both shore birds and cichlids were common at Cape Maclear. Further, shore birds foraged frequently in the shallow water between 0 and 0.5 m depth. Also, densities of the molluscivorous cichlid fishes (*Cyrtocara* [*Haplochromis*] *anaphymis*, *C. mola*, *C. placodon*, *C. sphaerodon*, and *Trematocranus microstoma*; see FRYER & ILES, 1972) were high between 1 and 15-m water depth in our study area (McKaye, unpublished data). Cichlids were observed attempting to feed on an extended foot or siphon of the larger *Lanistes* individuals; these attacks on large snails were generally unsuccessful (McKaye and Louda, personal observation). Additionally, stomach-content analysis showed small snails were particularly vulnerable to cichlid predators (McKaye and Louda, unpublished data). Temporal as well as spatial avoidance of the fish predation appeared important in recruitment and survival. Small individuals of both species were notably thin-shelled

Table 3

Apple snail density (number/25 m²) over the depth contour at Cape Maclear in southern Lake Malawi for each season sampled; highest density in each season is underlined.

Species Season	Depth (m)											
	1.5	4.6	7.7	10.8	13.9	17.0	20.1	23.1	26.3	29.4	32.5	35.6
A. <i>Lanistes nyassanus</i>												
Cool, dry 1980												
\bar{X}	8.9	<u>15.8</u>	6.6	7.8	3.9	7.2	5.0	5.8	6.8	8.0		
SE	1.34	2.53	0.73	1.14	0.59	1.20	0.78	0.65	0.77	1.30		
N	8	4	14	14	14	14	14	16	12	8	—	—
Warm, wet 1981												
\bar{X}	<u>18.3</u>	12.7	3.9	1.9	3.9	2.6	4.4	8.2	5.9			
SE	2.27	1.38	0.85	0.35	0.83	0.42	0.73	1.59	0.98			
N	12	12	8	8	8	8	8	12	8	—	—	—
Cool, dry 1981												
\bar{X}	4.4	2.9	3.8	<u>11.2</u>	5.2	4.3	5.5	3.3	7.2	5.3	5.4	6.5
SE	0.98	1.59	0.81	1.12	0.77	0.51	0.64	0.54	0.93	0.54	0.66	1.50
N	16	16	16	16	16	16	16	16	16	12	16	4
Warm, wet 1982												
\bar{X}	5.7	<u>7.6</u>	2.6	4.4	2.1	2.5	2.2	2.9	1.4	2.1	1.6	
SE	0.86	0.59	0.76	0.75	0.42	0.34	0.55	0.55	0.30	0.42	0.26	
N	16	16	16	16	16	16	16	16	16	16	16	—
B. <i>Lanistes solidus</i>												
Cool, dry 1980												
\bar{X}	4.6	<u>72.0</u>	0.2	0.2	0.0	0.1	0.1	0.0	0.0			
SE	0.62	9.34	0.11	0.13	0.00	0.08	0.08	0.00	0.00			
N	12	8	12	12	12	12	12	12	12	—	—	—
Warm, wet 1981												
\bar{X}	36.0	<u>55.2</u>	0.2	0.2	0.1	0.0	0.0	0.0	0.0			
SE	12.75	19.61	0.61	0.25	0.12	0.00	0.00	0.00	0.00			
N	10	12	8	8	8	8	8	8	8	—	—	—
Cool, dry 1981												
\bar{X}	13.6	<u>24.3</u>	0.2	0.2	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
SE	1.98	2.41	0.10	0.14	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00
N	16	16	16	16	16	16	16	16	16	16	16	16
Warm, wet 1982												
\bar{X}	7.4	<u>9.4</u>	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
SE	0.72	1.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
N	16	16	16	16	16	16	16	16	16	16	16	—

(WORLD HEALTH ORGANIZATION, 1977), extremely fragile (Louda, personal observation) and rare (Figure 2). Also, small, young snails were observed in systematic searches only in protected microhabitats, such as empty adult shells or among the vascular macrophyte stems. These individuals are highly susceptible to the molluscivorous cichlids present (LOUDA & MCKAYE, 1982; McKaye and Louda, unpublished data).

Our observations over the 20 months suggest that the

occurrence of both species was related to vascular macrophyte cover. *Potamogeton trichocoides*, the predominant macrophyte in August 1980, decreased from 25% cover to less than 1% cover between February and August, 1981 (Louda, unpublished data). At the same time the distribution and density of both species changed. Total density declined for both species by the warm, wet season of 1982 (Table 3), especially for *L. solidus*. The highest densities of *L. nyassanus* declined and shifted deeper by August

Lanistes size distributions by season: aperture length at sampling depths along the bottom profile at Cape Maclear, southern Lake Malawi, throughout the study, July 1980–March 1982; smallest and largest mean sizes along each seasonal transect are underlined once and twice, respectively.

[illegible]

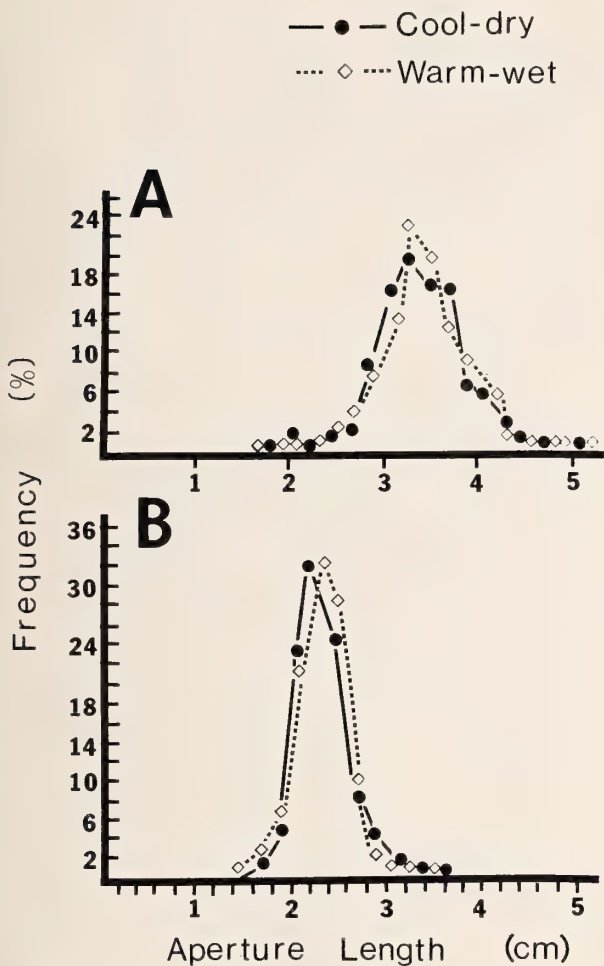


Figure 2

Frequency distribution of relative size (aperture length in cm) for each species at Cape Maclear for each season sampled in 1981 (● = cool-dry; ◇ = warm-wet). A. *Lanistes nyassanus*; B. *Lanistes solidus* (all N's > 500 per season).

1981 (Table 3A); those of *L. solidus* had halved but did not shift. These changes were correlated with the decline of macrophytes at 3–5 m depth (Pearson's rank correlation coefficient, $P < 0.05$).

Each species was associated with the macrophytes, but in different ways, rather than associated with each other. The observations suggest a refuge hypothesis for *L. nyassanus*. Maximal *L. nyassanus* densities occurred initially in and above the macrophyte bed at 3–5 m (Table 3A; LOUDA & MCKAYE, 1982). The smallest individuals of *L. nyassanus* occurred among the weeds, at 4.6 m during the first two sampling periods but deeper, at 10.8–13.9 m, after the weeds declined (Table 4A). Maximal density of *L. nyassanus* at any depth was lower after weed disappearance than before (Table 3A).

The refuge hypothesis for adults of *L. solidus* is less likely. Average size did not vary between snails in and outside the bed at 3–5 m (Table 4B). However, with the disappearance of the weeds by the cool dry season 1981, densities declined and became more equally divided between the two shallower depths (Table 3B). The weeds may provide a refuge for recruitment of young *L. solidus* since the only individuals less than 1.0 cm observed were found among the weed stems. An alternative hypothesis for the occurrence of adult *L. solidus* in the shallow water is derived from feeding observations. Although both species will feed on dead plant and animal matter, *L. solidus* scavenged significantly more frequently than *L. nyassanus* (Louda, unpublished data). Indeed, *L. solidus* can be "baited" with organic matter. The weed bed, besides providing a potential source of scavengable plant material, also acted as a trap for free floating items carried by the water current (Louda, personal observation). Thus, high density of adult *L. solidus* in the bed would reflect increased food availability.

In sum, we propose that the weed-bed microhabitat allowed upward extension of high densities of *L. nyassanus* by providing a refuge for smaller individuals and a potential recruitment site for young. Also, the weed bed led to a high density of adult *L. solidus* by providing a concentrated source of a sporadic resource, scavengable matter. With loss of the weed bed, dispersion and decline of both *Lanistes* populations occurred.

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The Recent Crassatellinae of the Eastern Pacific, with Some Notes on *Crassinella*

by

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Abstract. The three eastern Pacific species of the Crassatellinae belong in *Eucrassatella* Iredale, 1924. *Hybolophus* Stewart, 1930, is regarded as a synonym of this genus, as is the recently proposed but unavailable *Eucrassinella* Cruz, 1980. The rare *E. fluctuata* (Carpenter, 1864) occurs off the Channel Islands of southern California at a mean depth of 88 m; a synonym is the Plio-Pleistocene *Crassatellites lomitensis* Oldroyd, 1924. *Crassatella marginata* Keep, 1887, ex Carpenter MS, which has been synonymized with *E. fluctuata*, is instead based on specimens of the bernardinid genus *Halodakra*, perhaps *Halodakra salmonea* (Carpenter, 1864). *Eucrassatella gibbosa* (Sowerby¹, 1832) occurs from the Gulf of California to Peru at a mean depth of 32 m. Added to its synonymy are *Eucrassatella* (*Hybolophus*) *gibbosa* *tucilla* Olsson, 1932, and *Eucrassinella manabiensis* and *E. aequitorialis* Cruz, 1980. *Crassatella corbuloides* Reeve, 1842, which has been synonymized with *E. gibbosa*, is instead an Australian taxon. The Venezuelan *Eucrassatella antillarum* (Reeve, 1842) is synonymized with the eastern Pacific *E. digueti* (Lamy, 1917). In the eastern Pacific this species occurs at a mean depth of 45 m from the Gulf of California to Ecuador. Newly added to its synonymy is *Crassatella laevis* A. Adams, 1854, from the Caribbean. Lectotypes are selected for all of the synonymous taxa of *Eucrassatella*.

There has been an overrecognition of full, cognate species between the Panamic and Caribbean faunal provinces. Increased consideration should be given to the use of subspecies or describing the morphological differences between populations without naming them.

The Caribbean *Crassinella aduncata* Weisbord, 1964, is related to the eastern Pacific *C. adamsi* Olsson, 1961; *C. maldonadoensis* (Pilsbry, 1897) from Uruguay is very similar to the eastern Pacific *C. nuculiformis* Berry, 1940.

I HAVE PREVIOUSLY reviewed the members of the genus *Crassinella* occurring in the eastern Pacific, a genus in the crassatellid subfamily Scambulinae (COAN, 1979). Here I treat the subfamily Crassatellinae, which is represented in the eastern Pacific by the genus *Eucrassatella*. In particular, I have addressed the appropriate generic allocation for eastern Pacific members of this subfamily and the status of the subgenus *Hybolophus*; the validity of two taxa recently described from Ecuador, *Eucrassinella manabiensis* and *E. aequitorialis* Cruz; the proper home for *Crassatella marginata* Keep; the question of whether or not *Crassatella corbuloides* Reeve is a synonym of the eastern Pacific *Eucrassatella gibbosa* (Sowerby); the relationship of the Plio-Pleistocene *Crassatellites lomitensis* Oldroyd to the southern Californian *Eucrassatella fluctuata* (Carpenter); and the relationship of the eastern Pacific *Eucrassatella digueti* (Lamy) to the Caribbean *E. antillarum*. This led to consideration of how, in general, related taxa in the Panamic and Caribbean faunal provinces are handled nomenclaturally, and I have included here a discussion on this topic.

I have also included some information that has recently come to my attention about two western Atlantic species of *Crassinella* that are related to eastern Pacific taxa.

The Crassatellidae is an ancient and conservative family of marine bivalves, first appearing in the Paleozoic (BOYD & NEWELL, 1968; CHAVAN, 1969; MORRIS, 1978). The arrangement of its genera, including the Recent taxa, is in a less-than-satisfactory state. Previous reviews of the Recent crassatellid species of the world are by REEVE (1842, 1843), NYST (1847), TRYON (1872b), LÖBBECKE & KOBELT (1881, 1886), and LAMY (1917). BERNARD (1983:36) has recently listed the three eastern Pacific taxa of *Eucrassatella*.

CONVENTIONS AND ABBREVIATIONS

In the following treatment, the correct name is followed by a synonymy, information on type specimens and localities, notes on distribution and habitat, and an additional discussion.

The synonymies include all major accounts about the species, but not minor mentions in the literature. The entries are arranged in chronological order under each species-name, with changes in generic allocation and other notes provided in brackets at the end of the entry.

The following are the abbreviations of institutions used in the text:

AMNH—American Museum of Natural History

BM(NH)—British Museum (Natural History)

CASIZ—California Academy of Sciences, Department of Invertebrate Zoology

CASGTC—California Academy of Sciences, Geology Type Collection (numbers being replaced with CASIZ numbers)

LACM—Los Angeles County Museum of Natural History

USNM—United States National Museum of Natural History

A "pair" means the two valves of one individual.

Family CRASSATELLIDAE Férussac, 1822

Crassatellidae FÉRUSAC, 1822:xxxix, xlii; as "Crassatelles"

Subfamily Crassatellinae Férussac, 1822

Crassatella Lamarck, 1799

Crassatella LAMARCK, 1799:85–86; type species (monotypy): "*Macra cygnea* Chemnitz," LAMARCK, 1799 (*non Macra cygnus* GMELIN, 1791:3260, *ex* Chemnitz MS, a *Macra*), =*Venus ponderosa* GMELIN, 1791:3280, of which both *Crassatella gibba* LAMARCK, 1801:119, and *C. tumida* LAMARCK, 1805:408–409, are synonyms; middle Eocene, Paris Basin

Crassatellites KRÜGER, 1823:466 (unavailable; "ICZN Code," Arts. 20, 56b, because is based on *Crassatella* and modified only with an "ites" ending to indicate fossil taxa)

There are no known living members of the genus *Crassatella* in the eastern Pacific, but the name has been used for species in that province (as by MCLEAN, 1978:73), as has the unavailable generic unit *Crassatellites* Krüger.

Species of *Crassatella* have an opisthodontic ligament confined to the upper half of a broad hinge plate, and the inner ventral margins of their valves are denticulate. *Crassatella ponderosa* (Gmelin, 1791) is not uncommon in the middle Eocene of the Paris Basin, and the genus has been reported from the Cretaceous to the Recent (CHAVAN, 1969:N573).

The nomenclatural thicket surrounding the type species of *Crassatella* has been discussed by STEWART (1930:134–136), and by VOKES (1973:48–52), who said that he intended to file a petition with the International Commission on Zoological Nomenclature about it, but none has yet been published. Because it is a classic case of a misidentified type species, a petition would be required to validate the formulation above ("ICZN Code," Art. 70).

Species of *Crassatella* that occur in the Recent fauna are

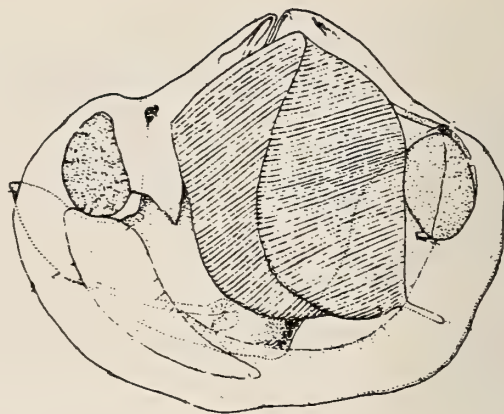


Figure 1

Bathytormus radiata (Sowerby); Singapore; drawing of gross anatomy after PELSENEER (1911). Note vertical orientation of ctenidial axis. Approximately $\times 2$.

placed into separate subgenera, including *Indocrassatella* CHAVAN, 1952:119 (type species by original designation: *C. indica* SMITH, 1895:265, of the Arabian Sea). HABE (1981:110) now ranks *Indocrassatella* as a full genus, including in it *I. oblonga* (YOKOYAMA, 1920:142–143; plt. 11, figs. 8, 9) from Japan. A second subgenus, *Riosatella* VOKES, 1973:52, occurs in the western Atlantic. Its type species, by original designation, *C. (R.) riograndensis* VOKES, 1973 (pp. 52–57; plt. 1, figs. 1–5), seems to be a synonym of *C. (R.) brasiliensis* (DALL, 1903a:101–102).¹

Several fossil taxa from eastern North America are referred to *Crassatella*, and on the Pacific Coast *C. washingtoniana* (WEAVER, 1912:32, plt. 4, fig. 42; plt. 5, fig. 51) has been assigned here as well (STEWART, 1930:137). As far as I know, none of these fossil taxa have been assigned to subgenera, and the arrangement and ranking of the named generic units near *Crassatella* awaits careful study.

The anatomy of *Crassatella* (*Indocrassatella*) *indica* has been briefly discussed but not illustrated by STOLICZKA (1871:291–292), RIDGEWOOD (1903:223), and WHITE (1942:64). PELSENEER (1911:37; plt. 13, fig. 1) discussed and illustrated the external anatomy of another crassatellid, *Bathytormus radiatus* (SOWERBY, 1825:7; ii–iii; plt. 1, fig. 2) from Singapore, and that figure is copied here (Figure 1). *Bathytormus* is conspicuously different from *Crassatella indica* and *Eucrassatella* (discussed below) in that the ctenidial axis is oriented almost dorso-ventrally.

Eucrassatella Iredale, 1924

Eucrassatella IREDALE, 1924:181, 202; type species (original designation): *Crassatella kingicola* LAMARCK, 1805:409, from King Island, northwest of Tasmania

¹ A still older name is possibly *Crassatella uruguayensis* SMITH, 1880 (pp. 321–322). RIOS (1975:212) synonymizes *C. riograndensis* with *C. uruguayensis*, incorrectly terming Smith's species "invalid."

Hybolophus STEWART, 1930:139; type species (original designation): *Crassatella gibbosa* Sowerby¹, 1832, from the eastern Pacific, discussed below

Eucrassinella CRUZ, 1980:66 (unavailable, no designated type species; "ICZN Code," Art. 13b)

Eucrassatella was erected by IREDALE (1924) for some Australian species that had previously been allocated to *Crassatella*. He argued that neither *Crassatella* nor *Crassatellites* were available for nomenclatural reasons. DARRAGH (1964, 1965a) has discussed the nomenclature and distribution of *E. kingicola* and other Australian members of this genus.

Members of *Eucrassatella* are medium-sized to large (to over 100 mm), with an even outline to produced posteriorly in some. The beaks are inflated in some species and flattened in others, and are prosogyrate to slightly opisthogyrate. The valves have prominent concentric folds, sometimes confined to the beaks but sometimes covering the entire shell surface. There is a dark brown periostracum in most species. Juvenile specimens are extraordinarily flattened laterally in some species.

The attachment of the internal ligament extends from the umbones almost to the ventral margin of the hinge plate. There are two cardinal teeth anterior to the resilium in the left valve and two in the right, although the anterior cardinal may be almost obsolete in the right valve. The cardinal teeth often have serrations on their anterior and posterior surfaces. The right valve has an elongate posterior lateral tooth that fits into a slot in the left valve; the ventral margin of this slot is often raised into a tooth. The left valve has an anterior lateral tooth that fits into a slot in the right valve; the ventral margin of this slot is also often raised into a tooth. DARRAGH (1965b) has discussed the incidence of hinge transposition in *Eucrassatella*. The pallial sinus is entire, and there are no denticulations along the inner ventral valve margins.

The external anatomy of *Eucrassatella* was discussed by WOODWARD (1854:300) and later illustrated by him (WOODWARD, 1866:466; fig. 259). His figure is reproduced here (Figure 2). Woodward's specimen was collected at "Sandy Cape," presumably in Queensland, and was referred by him to *E. pulchra* (REEVE, 1842:43).² RIDEWOOD (1903:223) later commented on the flat, homorhabdic ctenidia of the Australian *E. cumingi* (A. ADAMS, 1854a:90-91; plt. 16, fig. 1).

² Because Sandy Cape is outside the reported distribution of *E. pulchra* (see DARRAGH, 1964:8), the specimen discussed and illustrated by Woodward may have been another species, perhaps also *E. cumingi* (A. Adams). *Eucrassatella corbuloides* (REEVE, 1842:45), an Australian taxon not listed by Darragh, may be a senior synonym of the latter (type: BM(NH) 1953.4.15.9, holotype; length, 44.0 mm; height, 34.4 mm; thickness, 23.9 mm). Darragh (*in litt.*, 2 March 1983) now thinks that *E. cumingi*, *E. pulchra*, and *E. decipiens* (REEVE, 1842:42-43) may represent a cline from Perth, Western Australia, along the coasts of Northern Australia and Queensland, to northern New South Wales. Presumably, *E. corbuloides* would fit into this cline as well.

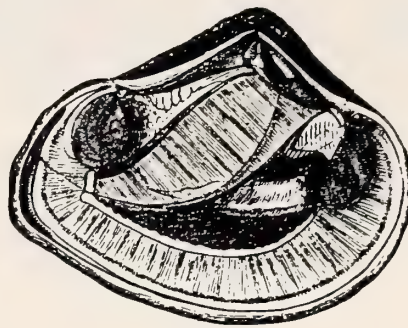


Figure 2

Eucrassatella "pulchra" (Reeve); Sandy Cape, Queensland, Australia; drawing of gross anatomy copied from WOODWARD (1866). Approximately $\times 1$.

Ridewood also said that he had studied the ctenidia of *Crassatella floridana* DALL, 1881:131, now regarded as a synonym of *Eucrassatella speciosa* (A. ADAMS, 1854b:94), from the western Atlantic. The identity of the material, which had been sent to him by Dall himself, was also confirmed by E. A. Smith. Ridewood found the ctenidia of the specimen to be strongly plicate and the foot to be "relatively huge saltatory." He suggested that these characters were so unique that workers might choose to separate this species from other crassatellids. However, HARRY (1966:86-87) recently examined a specimen of *E. speciosa* and found that the ctenidia are not plicated, leaving doubt about the identity of Ridewood's specimen. Harry also described other features of the anatomy of *E. speciosa*.

STEWART (1930) proposed *Hybolophus* as a subgenus of *Eucrassatella*, with the eastern Pacific *E. gibbosa* as its type species. The chief character he used to separate *Hybolophus* from the Australian nominal subgenus was the supposed opisthogyrate beaks of *E. gibbosa*, of "a large species from Lower California," and of *E. antillarum*. He said that *E. gibbosa* was "distinctly opisthogyrate," the Baja Californian species was "slightly opisthogyrate," and the Caribbean *E. antillarum* was, simply, "opisthogyrate." West American fossil taxa, on the other hand, he said lack backwards-pointing beaks.

Stewart also noted that the two living west American forms he studied differed from Australian material in that they had flattened umbones, but he also pointed out that *Eucrassatella kingicola* has umbones that are not as inflated as other Australian species of the genus. His somewhat ambivalent conclusion was that "Although none of the American species seem particularly closely related to *Eucrassatella*, I have not been able to discover any character by which they may all be separated from the Australian species."

DARRAGH (1965a:5), commenting on this question, said, "Species from the Central American Region (California to Peru and the West Indies) do not belong in *Eucrassatella* but in *Hybolophus*. . . . *Hybolophus* has opisthogyral

or orthogyral umbones, a sinuous ventral margin, and rather elongate anterior laterals."

None of the characters mentioned by Stewart or Darragh seems to be an adequate basis for distinguishing an eastern Pacific subgenus. The Californian *Eucrassatella fluctuata* has inflated, prosogyrate beaks and a more-or-less even ventral margin, and would thus have to be separately placed in *E. (Eucrassatella)*, as would a number of West Coast fossil taxa. The Australian *E. cumingi* sometimes has a sinuous posterior ventral margin (DARRAGH, 1964: plt. 2, fig. 9), and *E. corbuloides* (REEVE, 1842:45) has a still more sinuous posterior end.

I would not term the beaks of the Recent American species of *Eucrassatella* strongly opisthogyrate. Those of *E. gibbosa* are barely so, if at all. I would term those of what we have called "*E. digueti*" (presumably Stewart's large Baja Californian species) slightly prosogyrate. The beaks of the western Atlantic *E. speciosa* are flattened and orthogyrate.

In contrast to Darragh's claim, the anterior lateral of *E. gibbosa* in the left valve and its corresponding socket in the right valve are not conspicuously elongate. In fact, CHAVAN (1969:N576) characterizes the difference between the two taxa as being quite the opposite—short anterior laterals in *Hybolophus* and long anterior laterals in *Eucrassatella*. The length of the anterior laterals is of some use in separating species, however, as will be shown below.³

Thus, the differences between the Australian species of *Eucrassatella* and those of the eastern Pacific and western Atlantic are not sufficiently great or consistent to merit their subgeneric separation, and I regard *Hybolophus* as a synonym of *Eucrassatella*. Perhaps when the living and fossil taxa are studied in greater detail, two distinct lines will be more apparent.

Eucrassinella was proposed by CRUZ (1980) in combination with two new species. Both species are synonyms of *Eucrassatella gibbosa* (see below), and because the genus

is proposed without the designation of a type species, it must be regarded as unavailable ("ICZN Code," Art. 13b).

The three eastern Pacific species of *Eucrassatella* may be differentiated as follows:

- (1) Anterior lateral in left valve (and socket for it in right valve) elongate; posterior cardinal (just anterior to resilium) bifid, with a thin posterior lamella; beaks flattened; distinctly truncate posteriorly . . . *E. antillarum*
- (2) Anterior lateral in left valve (and socket in right valve) elongate; posterior cardinal not bifid, but with an indented posterior platform; beaks not flattened; very broadly and indistinctly truncate posteriorly *E. fluctuata*
- (3) Anterior lateral in left valve (and corresponding socket in right valve) short; posterior cardinal in right valve not bifid, with a flat posterior platform; beaks flattened; narrow posterior ridge present rather than a truncation *E. gibbosa*

A word of caution: the most variable feature of species of *Eucrassatella* is the degree of elongation of the posterior end, and unusually elongate specimens may be encountered in both *E. antillarum* and *E. gibbosa*. Other features are more reliable. Fossil taxa should be reexamined in light of the variability in posterior length among Recent material.

Eucrassatella fluctuata (Carpenter, 1864)

(Figures 3, 4, 5)

Astarte fluctuata Carpenter, 1864

CARPENTER, 1864b:611, 642 [1872:97, 128]

CARPENTER, 1866:209

TRYON, 1872b:246

SMITH, 1881:231

DALL, 1921:31 [*Crassatellites*]

OLDROYD, 1925:109 [*Crassatellites*]

BURCH, 1944:8; BURCH, 1945:11 [*Crassatella*]

WOODRING, *et al.*, 1946:81–82; 131 (plt. expl.); plt. 13, figs. 1–8 [*Eucrassatella*]

PALMER, 1958:81; 332 (plt. expl.); plt. 7, figs. 5–7 [*Eucrassatella*]

MCLEAN, 1969:73–74; fig. 40-3 [repr. 1978] [*Crassatella*]

MOUNT, 1974:38–40, 42–43; plt. 1, figs. 7–10 [*Crassatella*]

BERNARD, 1983:36 [*Eucrassatella (Hybolophus)*]

³ BOYD & NEWELL (1968:10; 1969:N908–N911) call into question the routine application of the Bernard and Munier-Chalmas system of numbering bivalve hinge teeth, particularly to the crassatellids, as by LAMY (1917), DARRAGH (1965a), and CHAVAN (1969).

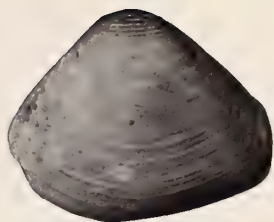
Explanation of Figures 3 to 10

Figures 3 to 5: *Eucrassatella fluctuata* (Carpenter). Figure 3. **Lectotype** (herein) of *Astarte fluctuata* Carpenter, length, 8.4 mm. Figure 4. Holotype of *Crassatellites lomitis* Oldroyd, length, 42.0 mm. Figure 5. Specimens from Catalina Island, Los Angeles Co., Calif.; 10 m; lengths, 43.5 mm and 42.2 mm; LACM 64-26 (illustrated by MCLEAN, 1969, 1978: fig. 40-3).

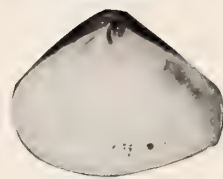
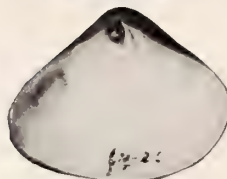
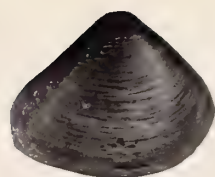
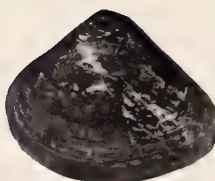
Figures 6 to 10: *Eucrassatella gibbosa* (Sowerby). Figure 6. **Lectotype** (herein) of *Crassatella gibbosa* Sowerby, length, 59.3 mm. Figure 7. Holotype of *Crassatellites rudis* Li, length, 46.9 mm. Figure 8. Holotype of *Eucrassatella gibbosa tucilla* Olsson, length, 66.6 mm. Figure 9. Holotype of *Eucrassinella manabiensis* Cruz, length, 13 mm; copied from CRUZ (1980). Figure 10. Holotype of *Eucrassinella aequitorialis* Cruz, 18 mm; copied from CRUZ (1980).



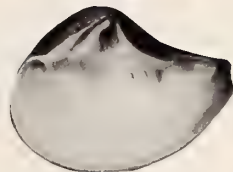
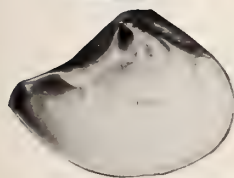
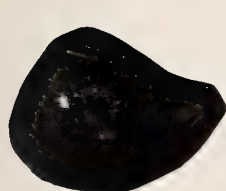
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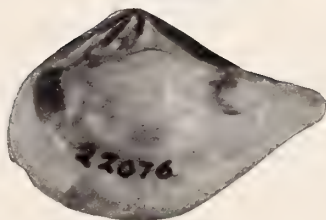
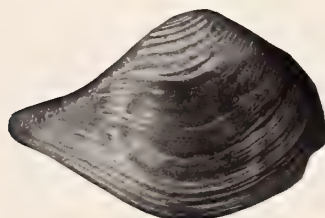
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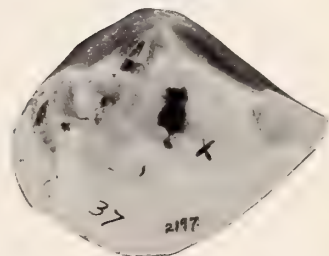
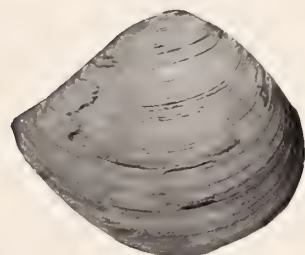
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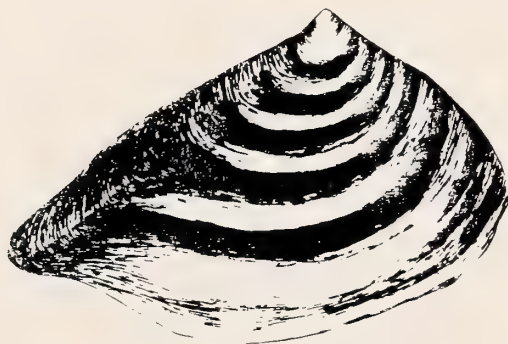
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10

Crassatellites lomitensis Oldroyd, 1924

OLDROYD, 1924:10; pl. C

GRANT & GALE, 1931:271

WOODRING *et al.*, 1946:81 [as a synonym of *Eucrassatella fluctuata*]

MOUNT, 1974:37–44; pl. 1, figs. 1–6 [*Crassatella*]

Type material and localities:

A. fluctuata—USNM 819749, **lectotype** herein, a right valve, from Calif. State Coll. 1060; length, 8.4 mm; height, 6.5 mm; thickness, 1.6 mm (Figure 3). Carpenter evidently had two right valves, so the specimen in the USNM cannot be a holotype, as indicated by PALMER (1958). The second specimen has not come to light in either the USNM, or at the University of California at Berkeley (David Lindberg, oral communication, 14 March 1983).

Catalina Id., Los Angeles Co., California (about 33°27'N; 118°28'W); 73 m; James G. Cooper; June 20–26, 1863.

C. lomitensis—Univ. Calif. Riverside 6621/1, holotype, a left valve; length, 42.0 mm; width, 33.7 mm; thickness, 11.7 mm (Figure 4). OLDROYD (1924) implied that the type specimen included both valves but illustrated only this left valve, and a right valve was not located by Mount (1974).

Lomita Lime Quarry, southern part of Lomita, Los Angeles Co., California (33°47'N; 118°20'W); Lomita Marl; lower Pleistocene; S. Maus Purple.

Description:

Small for genus, to 53.2 mm in length (LACM 89202; off San Clemente Id., Calif.); shell trigonal to longer posteriorly, length 1.26 times height (SD, ± 0.08 ; N = 11); moderately inflated, thickness 0.58 times height (SD, ± 0.04 ; N = 12); posterior end only slightly truncate, not produced; beaks inflated, prosogyrate, with concentric undulations that continue onto posterior slope; undulations often confined to beaks, but sometimes over entire valve. Lunule and escutcheon relatively short, shallow. Periostracum dark; shell surface under periostracum with dark, radial bands.

Left valve with a fairly thin posterior cardinal and an elongate anterior lateral. Posterior cardinal of right valve attached dorsally to anterior cardinal and with a postero-ventral pocket, not bifid as in *E. antillarum*; elongate slot present for anterior lateral of left valve. Hinge teeth not conspicuously serrate, as in *E. gibbosa* and *E. antillarum*.

Pallial line curving more sharply upward at its posterior end than that in *E. gibbosa*. Pit for pedal elevator under beaks not as deep as that in *E. gibbosa*.

The type specimen being a single juvenile valve, I have illustrated here both valves of adult Recent specimens (Figure 5).

Distribution and habitat:

From off Santa Rosa Id. (34°5'N; 120°2'W) (USNM 211883) and off Santa Cruz Id. (34°3'5"N; 119°57'30"W) (LACM 68-128), Santa Barbara Co., to off Santa Catalina Id. (33°25'30"N; 118°30'33"W) (CASIZ 036682) and probably as far south as to off northwest end of San Clemente Id. (about 33°N; 119°W) (LACM 89202), Los Angeles Co., California; 10 to 320 m, with a mean depth of 88 m. No bottom types are recorded, but it probably occurs among rubble. This species is rare, and I have seen only 18 Recent lots.

It is recorded in the lower Pliocene of Los Angeles Co. (WINTERER & DURHAM, 1962:302), the upper Pliocene of Orange Co. (ZINSMEISTER, 1971:122; MOUNT, 1974: 41); and the lower Pleistocene of Los Angeles Co. (OLDROYD, 1924:10; SCHENCK, 1945:513; WOODRING *et al.*, 1946:81–82), all in California.

Discussion:

Based chiefly on a single lot from off Catalina Island (Univ. California Riverside 7279/1-3), MOUNT (1974) argued that the Recent *Eucrassatella fluctuata* differs from the Plio-Pleistocene *E. lomitensis* in that it has (1) a different profile, (2) higher, more pronounced beaks that are closer to the anterior end, and (3) concentric sculpture that is confined to the umbones. However, this species is rare, and having examined most of the extant Recent material in public collections, I have noted considerable variability in these features.

Some specimens have a more elongate posterior end, but many shells are closer to triangular. Some specimens have the undulating concentric sculpture confined to the beaks, whereas it covers most of the shell in other material. Mount also mentions but does not specify differences in the hinge, but his excellent description of the hinge of "*E. lomitensis*" fits Recent material of *E. fluctuata* as well.

In describing *Crassatellites lomitensis*, Oldroyd said, "inner margin crenulated." I have seen no sign of crenulations on the specimens I have studied, including the holotype.

BERNARD (1983:36) synonymizes "*Crassatella marginata* Keep, 1888" with this species, terming it a *nomen nudum*. It does not belong here, and this is discussed below.

Eucrassatella gibbosa (Sowerby, 1832)

(Figures 6 to 11)

Crassatella gibbosa Sowerby¹, 1832

SOWERBY¹, in BRODERIP & SOWERBY¹, 1832:56

REEVE, 1841:63; pl. 44, fig. 2

REEVE, 1842:45

REEVE, 1843:pl. 1, figs. 1a, 1b

HANLEY, 1843:37; pl. 12, fig. 16; 1856:341

NYST, 1847:122–123

C. B. ADAMS, 1852a:516 [1852b:292]

CARPENTER, 1857a:280, 297

- CARPENTER, 1864a:30 [1872:204]
 CARPENTER, 1864b:537, 620, 669 [1872:23, 106, 155]
 NELSON, 1870:203; ?plt. 7, fig. 9 [in part; see OLSSON, 1932:88]
 TRYON, 1872b:250
 LÖBBECKE & KOBELT, 1881:8-9; plt. 3, figs. 3, 3a, 4; KOBELT, 1886:41 (plt. expl.)
 LAMY, 1917:218-219
 HERTLEIN & STRONG, 1946:103 [*Crassatellites* (*Hybolophus*)]
 HERTLEIN & STRONG, 1955:181-182 [*Crassatellites* (*H.*)]
 KEEN, 1958:82, 83; fig. 158 [*Crassatella* (*H.*)]
 OLSSON, 1961:179-180; 498 (plt. expl.); plt. 25, figs. 1-1b [*Eucrassatella* (*H.*)]
 PARKER, 1964:117, 159, 168; plt. 4, figs. 18a, 18b [*Crassatella* (*H.*)]
 KEEN, 1971:104, 105; figs. 230 [*Eucrassatella* (*H.*)]
 BERNARD, 1983:36 [*E. (H.)*]
 [not to be confused with *Crassatella gibba* Lamarck, 1801:119, or with *C. gibbosula* Lamarck, 1805:410-411]
Crassatellites rudis Li, 1930
 LI, 1930:257; 286 (plt. expl.); plt. 3, figs. 16
 PILSBRY, 1931:429-430; 440 (plt. expl.); plt. 41, figs. 9, 10 [as a form of *C. gibbosus*]
 PARKER, 1964:120, 159; plt. 5, figs. 20a, 20b [as both *Eucrassatella* and as *Crassatella* (*Hybolophus*), in each case as a form of *gibbosa*]
Eucrassatella (*Hybolophus*) *gibbosa* *tucilla* Olsson, 1932
 OLSSON, 1932:88; 228 (plt. expl.); plt. 6, fig. 6
 PILSBRY & OLSSON, 1941:56
Eucrassinella manabiensis Cruz, 1980
 CRUZ, 1980:67-68, 72, 73; figs. 5, 6 [figs. 1 and 2 are *Eucrassatella antillarum*]
Eucrassinella aequatorialis Cruz, 1980
 CRUZ, 1980:68, 72, 73; figs. 3, 4, 7
Crassatella digueti Lamy, auctt., non Lamy, 1917
 DURHAM, 1950:70; 161 (plt. expl.); plt. 16, figs. 5, 13

Type material and localities:

- C. gibbosa*—BM(NH) 1953.4.15.15, **lectotype** herein, pair, the larger specimen figured by REEVE (1843); length, 59.3 mm; height, 44.5 mm; thickness, 31.4 mm (Figure 6). The specimen was labeled "holotype," but it is clear that Sowerby had more than one specimen. BM(NH) 1842.5.10.1586, probable **paralectotype**; length, 41.5 mm; height, 25.9 mm; thickness, 19.3 mm.
 Either Jipijapa [Puerto de Cayo], Manabi Prov. (1°20'S; 80°45'W); or Santa Elena, Guayas Prov. (2°11'S; 80°52'W), Ecuador, 20 m; sandy mud; Hugh Cumming.
C. rudis—AMNH 22076, holotype, a right valve; length, 46.9 mm; height, 31.0 mm; thickness, 9.9 mm (Figure 7). The specimen was labeled "syntype," but there is no evidence of there having been any other specimens in the lot (Batten, *in litt.*, 1 March 1983).
 Mouth of Río Grande [now the Panama Canal], near La Bocca, about 1.6 km offshore, Panama Bay, Panama (about 8°55'N; 79°33'W); 3-12 m; mud; Donald F. MacDonald, 1907. "lower Miocene," but really Re-

E. gibbosa *tucilla*—Paleontological Research Institution 2197, holotype, a broken right valve; length, 66.6 mm; height, 53.3 mm; thickness, 25.6 mm (Figure 8).

Quebrada Tucillal, Zorritos, Tumbes Prov., Peru (3°40'S; 80°40'W); Tumbes Formation; upper Miocene.

E. manabiensis—Mus. Biol. Mar., Inst. Oceanográf. de la Armada, Guayaquil, Ecuador; holotype; pair; length, 13 mm; height, 8 mm; thickness, 2 mm (Figure 9; reproduced from CRUZ, 1980: figs. 5, 6). Paratypes, USNM 768218 & 768219. The paratype illustrated in Cruz's figures 1 and 2 appears to be a juvenile of *Eucrassatella antillarum*.

Type locality not made clear in original publication, but according to Cruz (*in litt.*, 23 March 1983) the holotype came from Machalilla, Manabi Prov., Ecuador (1°27'S; 80°46'W); between 11 and 17 m.

E. aequatorialis—Mus. Biol. Mar., Inst. Oceanográf. de la Armada, Guayaquil, Ecuador; holotype, pair; length, 18 mm; height, 11 mm; thickness, 6 mm (Figure 10; reproduced from CRUZ, 1980:fig. 7).

Machalilla, Manabi Prov., Ecuador (1°27'S; 80°46'W); on beach.

Description:

Medium-sized for genus, to 87.4 mm in length (CASIZ 036002; Guaymas, Sonora, Mexico); shell elongate, from equilateral to longer posteriorly, length 1.45 times height (SD, ± 0.09 ; N = 19); inflated, especially anteriorly, thickness 0.67 times height (SD, ± 0.05 ; N = 19); posterior end with a very narrow truncation, forming a sharp ridge on many specimens; posterior end very produced in some specimens; beaks flattened, orthogyrate to slightly opisthogyrate, with prominent concentric folds that terminate at posterior ridge; rest of surface with low, irregular growth lines. Lunule and escutcheon relatively short and deep. Periostracum dark brown; shell surface under periostracum brown, sometimes with dark radial rays.

Left valve with a short anterior lateral. Posterior cardinal of right valve rarely attached to anterior cardinal, with a postero-ventral shelf, not bifid, as in *E. antillarum*; short pocket present for anterior lateral of left valve. Hinge teeth serrate, serrations larger than those in *E. antillarum*.

Pallial line curving evenly upward toward posterior adductor muscle scar. Pit for pedal elevator under beaks unusually deep.

The soft parts (Figure 11) are similar to those of *Eucrassatella "pulchra"* (Figure 2).

Distribution and habitat:

Bahía San Juanico, outer coast of Baja California Sur, Mexico (26°15'N; 112°27'20"W) (LACM 71-180), throughout the Gulf of California, to Paita, Piura Prov., Peru (5°5'S; 81°7'W) (USNM 48447; OLSSON, 1961:180); 5 to 110 m, with a mean depth of 32 m; most records

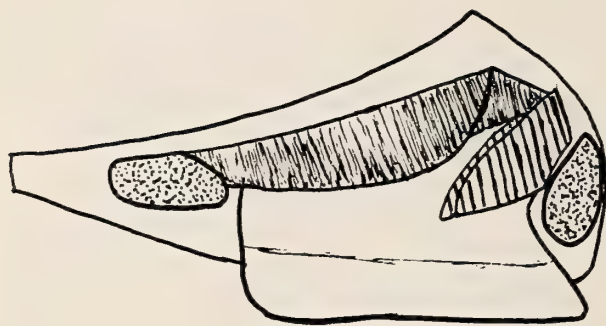


Figure 11

Eucrassatella gibbosa (Sowerby); Puerto de la Concordia, Guatemala; 18 m; ANSP 317727. Sketch of positions of ctenidia, palps, and foot. Approximately $\times 2$.

suggest that the species occurs on sand bottoms, although mud is also recorded at two stations. BERNARD (1983:36) reports this species from the Galápagos Islands, but I have not seen any material from there. This is the most common of the three species, and I have seen 167 Recent lots.

This species has been reported from the upper Miocene of Peru (NELSON, 1870:203; OLSSON, 1932:88) and from the Pliocene of Ecuador (PILSBRY & OLSSON, 1941:56) (the last two references as *E. gibbosa* *tucilla*); from the Pleistocene of the Burica Peninsula in Panama (OLSSON, 1942:162) and of Bahía de Santa Inez, Baja California Sur (DURHAM, 1950:70, as *C. digueti*). It may also be responsible for the record of "*Crassatella* n. esp. af. *gibbosa*" from the Pliocene of Punta Concepción, Baja California Sur (WILSON, 1948a:35; 1948b:1780).

Discussion:

PILSBRY (1931) was the first to recognize that Li's *Crassatellites rudis* was actually from the Recent fauna, not from the Miocene as Li had thought. It is nothing more than a rostrate specimen of *E. gibbosa*.

Olsson's claims for the uniqueness of *E. g. tucilla* are that this subspecies is (1) larger, (2) less convex, (3) less pointed posteriorly, and (4) has straighter, less contracted postero-dorsal submargins. It is certainly not true that it is larger, the largest Recent specimen being some 17 mm longer than the largest specimens attributed to Olsson's subspecies. Large Recent specimens are generally both less convex and less pointed, making their postero-dorsal slope less convex.

Whereas Cruz's new genus, *Eucrassinella*, is unavailable, his two new species are. However, both holotypes are juvenile specimens of this species.

BERNARD (1983:36) has synonymized *Crassatella corbuloides* Reeve, 1842, with this species, but it is instead from Australia (see footnote 2).

Crassatellites subgibbosus HANNA, 1926 (pp. 463-464; 500; plt. 28, figs. 1-4) from the Imperial Formation of southern California may prove to be a synonym of *Eucrassatella gibbosa*. STANTON (1966:28-29; 24; plt. 5, figs. 9-12) reports *E. subgibbosa* from the upper Miocene Castaic Formation, also in southern California, listing some differentiating characters that I find unconvincing. However, the material available to me from either locality is insufficient for a definitive conclusion to be drawn.

There are several other fossil taxa from the Americas that may be related to this species, but it is beyond the scope of this paper to determine which are closest or to elucidate their nomenclature. Several of these were recently discussed by WOODRING (1982:633-634).

Eucrassatella antillarum (Reeve, 1842)

(Figures 12 to 16)

Crassatella undulata Sowerby¹, 1832; non Say, 1824; non (Lamarck, 1801)

SOWERBY¹, IN BRODERIP & SOWERBY¹, 1832:56
REEVE, 1842:44

REEVE, 1843:plt. 1, figs. 2a, 2b

HANLEY, 1843:37; plt. 12, fig. 24; 1856:341

NYST, 1847:128-129

CARPENTER, 1857a:297

TRYON, 1872b:251

LÖBBECKE & KOBELT, 1881:11-12; plt. 4, figs. 3, 3a;

KOBELT, 1886:41 (plt. expl.)

[non Say, 1824:142; plt. 11, figs. 2]

[non *Crassatella undulata* (LAMARCK, 1801:120)]

Crassatella antillarum Reeve, 1842

REEVE, 1842:44-45

REEVE, 1843:plt. 2, fig. 8

HANLEY, 1843:37

NYST, 1847:120-121

CHENU, 1862:131; fig. 623

TRYON, 1872b:248

LÖBBECKE & KOBELT, 1881:7-8; plt. 3, figs. 1, 2, 2a;

KOBELT, 1886:41 (plt. expl.)

DALL, 1903b:1475 [*Crassatellites*]

LAMY, 1917:216-217; 202, figs. [*Crassatella*]

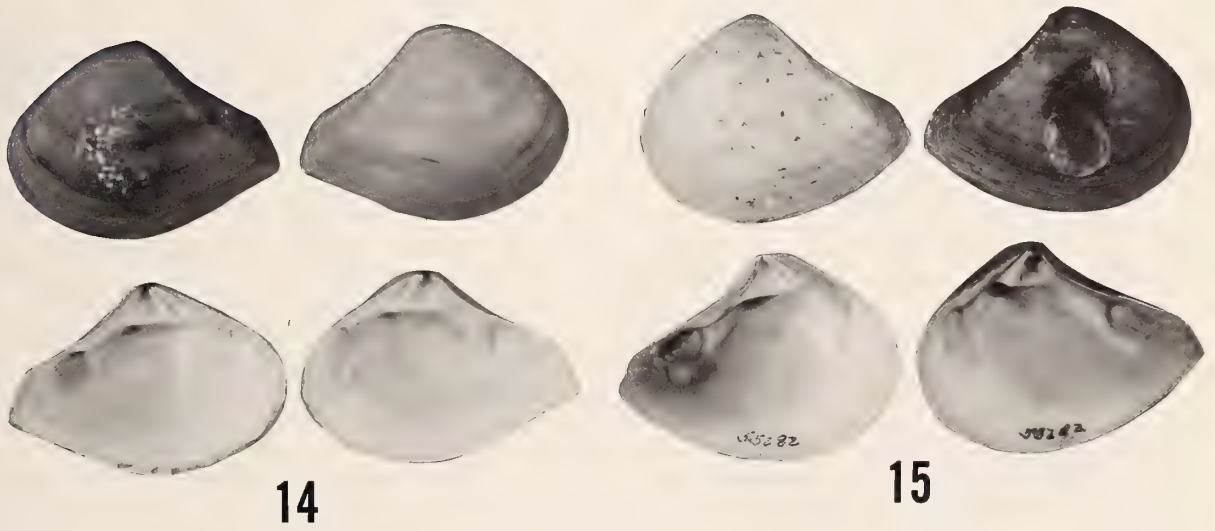
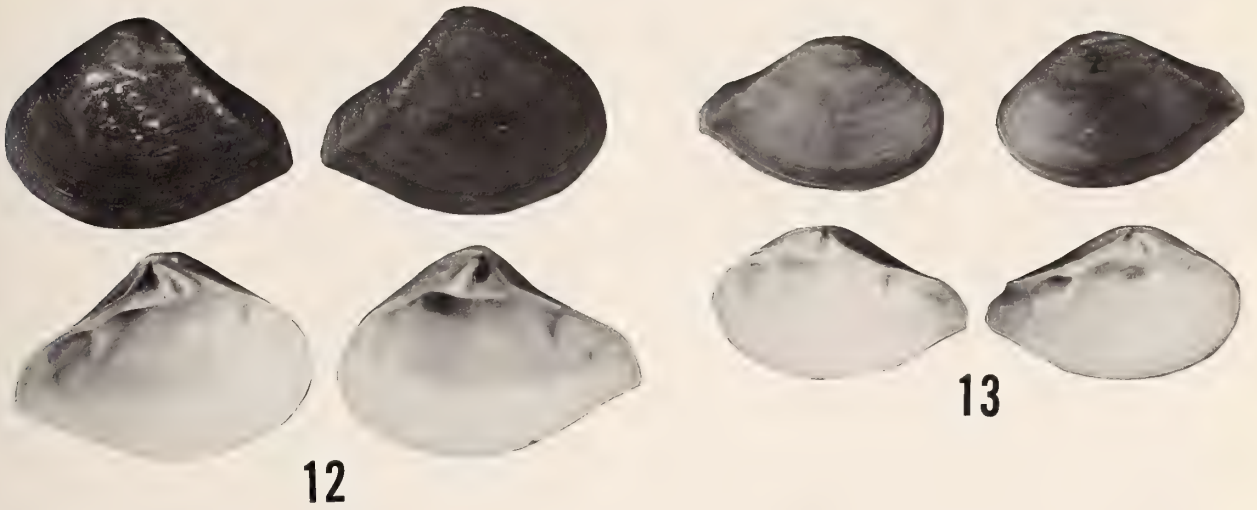
GRANT & GALE, 1931:271; 906 (plt. expl.); plt. 13, figs. 7a, 7b [*Crassatellites*]

WEISBORD, 1964:194-197; 514 (plt. expl.); plt. 25, figs. 9, 10 [*Eucrassatella* (*Hybolophus*)]

Explanation of Figures 12 to 16

Figures 12 to 16: *Eucrassatella antillarum* (Reeve). Figure 12. **Lectotype** (herein) of *Crassatella antillarum* Reeve, length, 80.0 mm. Figure 13. **Lectotype** (herein) of *Crassatella undulata* Sowerby, length, 66.6 mm. Figure 14. **Lectotype** (herein) of *Cras-*

satella laevis A. Adams, length, 42.5 mm. Figure 15. Holotype of *Crassatella adelinae* Tryon, length, 75.0 mm. Figure 16. Holotype of *Crassatellites laronus* Jordan, length, 77.5 mm.



GIBSON-SMITH & GIBSON-SMITH, 1979:28 [*E. (H.)*]
[note: "antillarum" is a noun meaning "of the Antilles"
and thus does not change its ending with the gender
of the generic name.]

Crassatella rostrata Lamarck, *auctt.*, non Lamarck, 1818

DELESSERT, 1841:plt. 4, figs. 2a, 2b, 3a, 3b

[non LAMARCK, 1818:482 (LAMARCK, 1805:408, is a *nomen nudum*), an Asian *Bathytormus*]

Crassatella laevis A. Adams, 1854

A. ADAMS, 1854b:94

TRYON, 1872b:250

LÖBBECKE & KOBELT, 1881:9-10; ?plt. 3, figs. 5, 5a;

KOBELT, 1886:37; 41 (plt. expl.)

LAMY, 1917:217

[not preoccupied by *C. laevis* HOENINGHAUS, 1831:162,
a *nomen nudum*]

Crassatella adelinae Tryon, 1872

TRYON, 1872a:130; plt. 6, figs. 1, 1a

TRYON, 1872b:249

WEISBORD, 1964:195, 197 [as a synonym of *E. (H.)*
antillarum]

Crassatella digueti Lamy, 1917; new name for *C. undulata*
Sowerby, 1932; non Say, 1824; non (Lamarck,
1801)

LAMY, 1917:217-218

HERTLEIN & STRONG, 1946:102-103 [*Crassatellites (H.)*]

KEEN, 1958:82, 83; fig. 157 [*Crassatella (H.)*]

OLSSON, 1961:180; 498 (plt. expl.); plt. 25, fig. 2 [as
Eucrasatella (H.) "digueti"]

KEEN, 1971:104, 105; fig. 229 [*E. (H.)*]

BERNARD, 1983:36 [*E. (H.)*]

Crassatellites laronus Jordan, 1932

JORDAN, 1932:9-10

JORDAN, 1936:124-125; 164 (plt. expl.); plt. 17, figs.
6, 7

DURHAM, 1950:70-71; 161 (plt. expl.); plt. 16, figs. 8,
14

HERTLEIN & STRONG, 1946:102 [as a synonym of *C.*
(H.) digueti]

Crassatella gibbosa Sowerby, *auctt.*; non Sowerby, 1832

KOBELT, 1886:34; 41 (plt. expl.); plt. 9, figs. 1

Eucrasinella manabensis Cruz, 1980 [in part]

CRUZ, 1980:72, figs. 1, 2

C. laevis—BM(NH) 1983.33/1-3, **lectotype** herein, pair;
length, 42.5 mm; height, 30.0 mm; thickness, 17.8 mm
(Figure 14). The lot also contains two **paralectotypes**,
one 31.4 mm in length, the other 27.7 mm in length.

Le Guaira, Federal Dist., Venezuela (10°36'N;
66°56'W); M. Le Marie; Cuming Coll.

C. adelinae—ANSP 55282, holotype, pair; length, 75.0
mm; height, 56.9 mm; thickness, 27.7 mm (Figure 15).

Locality unknown. WEISBORD (1964: 197) says, "The
habitat of Tryon's *E. adelinae* was unknown when that
species was described in 1872, but it was subsequently
determined to be also from Margarita Island in Vene-
zuela."

C. laronus—CASIZ 036680 (formerly CASGTC 5593),
holotype, a right valve; length, 77.5 mm; height, 54.6
mm; thickness, 12.8 mm (Figure 16).

West anchorage, near the salt works, Isla San José,
Baja California Sur (about 24°53'N; 110°35'W); CAS
Loc. 23809; on beach; Fred Baker.

Description:

Large for genus, to 105.2 mm in length (Paul Stillians
Coll., according to DRAPER, 1980: 25; Bahía de los An-
geles, Baja California Norte, Mexico); shell elongate, al-
most always longer posteriorly, length 1.49 times height
(SD, ± 0.09 ; N = 16); moderately inflated, thickness 0.59
times height (SD, ± 0.06 ; N = 16), less so than *E. gibbosa*;
posterior end with a broad truncation and a distinctly set
off posterior slope; posterior end produced in many spec-
imens, "pinched off" by an indentation in some; beaks
orthogyrate or very slightly opisthogyrate, with prominent
concentric folds which end at anterior margin of posterior
slope; rest of surface with low, irregular growth lines.
Lunule and escutcheon relatively shallow; lunule elongate
on most specimens. Periostracum dark brown; shell sur-
face under periostracum sometimes with dark brown ra-
dial bands; some specimens with radial bands broken into
brown chevrons; young specimens with flecks of brown.

Left valve with an elongate anterior lateral. Posterior
cardinal of right valve not attached to anterior cardinal,
but bifid, with a narrow ridge next to resilium (the pos-
terior cardinal of left valve fits between these two por-
tions); elongate pocket present for anterior lateral of left
valve. Teeth serrate; serrations finer than those in *E. gib-
bosa*.

Distribution and habitat:

Venezuela: from the west coast of the Peninsula de Pa-
raguaná, Falcon (about 70°W), to Isla de Margarita,
Nueva Esparta (about 64°W) (J. Gibson-Smith, *in litt.*,
28 Dec. 1982); from 3 to 8 m, but presumably also oc-
curring somewhat deeper; sand. It is not common in the
Caribbean, and I have seen only 15 lots; Gibson-Smith
knows of 4 more lots.

Eastern Pacific: from Cabo San Lucas, Baja California
Sur, Mexico (20°8'N; 110°W) (LACM 66-12 & 66-14;

Type material and localities:

C. undulata Sowerby—BM(NH) 1953.4.15.12, **lectotype**
herein, pair, probably the measured specimen and that
figured by REEVE (1843); length, 66.6 mm; height,
41.5 mm; thickness, 25.0 mm (Figure 13). BM(NH)
1953.4.15.12, a **paralectotype**; length, 23.4 mm; height,
14.2 mm; thickness, 7.4 mm.

Puerto Portrero, Guanacaste Prov., Costa Rica
(10°27'N; 85°48'W); 20 m; sandy mud; Hugh Cuming.

C. antillarum—BM(NH) 1953.4.15.10, **lectotype** herein,
pair, the measured syntype, which was figured by REEVE
(1843); length, 80.0 mm; height, 57.0 mm; thickness,
32.6 mm (Figure 12). BM(NH) 1953.4.15.11, a **para-
lectotype**; length, 82.3 mm; height, 56.4 mm; thickness,
27.3 mm.

Isla Margarita, Nueva Esparta, Venezuela (about
11°N; 64°W); "dredged up in the pearl-fisheries";
Cuming Coll.

CASIZ 036001; USNM 3984 & 12586), throughout the Gulf of California, to Playas, Guayas Prov., Ecuador (2°39'S; 87°52'W) (CASIZ 033528); 5 to 206 m, with a mean depth of 45 m; almost all recorded bottom types indicate sand or gravel. This species is not as common as *E. gibbosa*; I have seen 84 lots from the eastern Pacific.

This species is also known from the Pliocene of Venezuela (WEISBORD, 1964:196–197; GIBSON-SMITH & GIBSON-SMITH, 1979:28). The Gibson-Smiths suggest that the Mare Formation material might be a recognizable subspecies, differing from Recent specimens in being more elongate, and in having a straighter postero-dorsal margin and a more pointed anterior end.

In the eastern Pacific, this species has been reported as a fossil from Baja California Sur—from the Pliocene or Pleistocene of Santa Rosalia (GRANT & GALE, 1931) and from the Pleistocene of Isla Coronado (DURHAM, 1950, as *Crassatellites laronus*), Punta El Pulpito (HERTLEIN, 1957:63, as *Crassatella digueti*); and Bahía Magdalena (JORDAN, 1936, as *Crassatellites laronus*).

I am not certain which earlier fossil species is closest to *Eucrassatella antillarum*. A possible candidate is *E. nelsoni* (GRZYBOWSKI, 1899:639; 663 (plt. expl.); plt. 19, figs. 2, 2a) from the Miocene of Peru (see OLSSON, 1932:87–88; 228; plt. 6, figs. 1, 4).

Discussion:

REEVE (1842, 1843) discussed *Crassatella antillarum*, and noted that it was similar to *C. undulata* Sowerby but did not offer any characters to separate the two. LÖBBECKE & KOBELT (1881) also stressed the similarity of these species but failed to point to differentiating characteristics. GRANT & GALE (1931) used the name *Crassatellites antillarum* for Pacific Coast fossil specimens from Baja California.

After examining the material available to me, I am unable to find features upon which eastern Pacific material can be reliably separated. The average specimen of *Eucrassatella antillarum* from the Venezuelan coast may be more produced posteriorly than the eastern Pacific *E. digueti*, a feature noted by LAMY (1917:217) in the material he studied, but both long and short forms are found in both provinces, and, in fact, the lectotype of *C. undulata* Sowerby (Figure 13) is more produced posteriorly than is the lectotype of *C. antillarum* (Figure 12).

Crassatella laevis A. Adams, 1854b, described from Venezuela, sounded as if it might be a synonym of this species, so I borrowed the type material from the British Museum, and it confirmed my suspicion. Adams gave no measurements of his specimens and reversed the anterior and posterior ends in his description.

With the Caribbean taxon comes the synonym *Crassatella adelinae* Tryon, 1872, described from an unknown locality and synonymized by WEISBORD (1964). Caribbean material was also illustrated as "*Crassatella rostrata* Lamarck" by DELESSERT (1841), but NYST (1847:126–127), LAMY (1913:104; 1917:221–223; plt. 6, fig. 4), and

others have demonstrated that this was an error and that Lamarck's species is really from Asia.

Crassatella undulata Sowerby, 1832, is a primary homonym of *C. undulata* Say, 1824, from the Miocene of Virginia.⁴ *Crassatella digueti* Lamy, 1917, was proposed as a replacement name and thus has the same type specimens as Sowerby's species.

Crassatellites laronus Jordan, 1932, is unquestionably another synonym. It was differentiated from *Crassatella undulata* Sowerby as being thinner and less rostrate and as having a straighter postero-dorsal margin, character states well within the range of variability of this species.

Some biogeographic comments:

There is great inconsistency in how various workers nomenclaturally handle related taxa between the Caribbean and Panamic faunal provinces. For the most part, populations in the two provinces that differ in only minor ways morphologically are regarded as separate species, which are properly termed "cognates" or "homologues."⁵ Sometimes the morphological differences are so minor that, were the two populations to occur within a single province, the differences would be regarded merely as variation within a single taxon. (In the case of *Eucrassatella antillarum*, I have not been able to find sufficient differences between the populations in the two provinces to regard the names involved as anything but synonyms.)

Intermediate paths are possible between the recognition of full, cognate species and a single species with disjunct, undifferentiated populations—(1) to use the subspecific level, or (2) merely to describe the morphological differences between the populations without recognizing them as separate taxonomic units.

Workers on marine mollusks have not often relied upon the subspecific option across the Panama land barrier, and, in general, few subspecies are recognized among marine mollusks, in part because the pelagic larvae of many forms ensure wide distributions within habitable territory as well as the liberal mixing of genetic material. Whereas the trans-Panama situation meets the criterion of geographic separation required of most subspecies, its absolute and long standing nature—3.1 million years, according to KEIGWIN (1978)—has made some workers hesitant

⁴ It is also a secondary homonym of *Crassatella undulata* (LAMARCK, 1801:120), which was first proposed in the genus *Paphia* and later reassigned to *Crassatella* by LAMARCK (1805:408). Lamarck's species is a synonym of *Crassatella contraria* (GMELIN, 1791:3277), from West Africa.

⁵ Earlier literature used the term "analogues," which is clearly a misuse of this word since it implies a lack of phylogenetic relationship. There remains a tendency to search out and list pairs of so-called cognates between the Panamic and Caribbean faunal provinces without sufficient knowledge of the groups involved, and I harbor doubts about a number of the cognate pairs listed in the useful compilation of VERMEIJ (1978:269–278).

about invoking subspecies. However, for many groups of marine mollusks, this is not a very long time at all.

In two of the three cases in which I have previously used subspecies among marine bivalves, there were relatively sharp morphological breaks corresponding to geographic constrictions, and I concluded that gene flow was significantly restricted at those points. The third case involved an 1300-km gap between morphologically differing populations. Subspecies have sometimes been used in the eastern Pacific for isolates on offshore islands.

The key decision that a systematist must make is whether or not, in the absence of experimental evidence or other direct measures of genetic divergence, interbreeding and gene flow are occurring or could occur between populations. Judgments about this often have to be made on a case-by-case basis by means of analogies about the systematic importance of morphological differences among other species in the genus or family involved. This is, of course, indirect evidence, and the marine mollusks have many examples both of species within single genera that are scarcely distinguishable morphologically and of single species with astounding ranges of variability.

With regard to the Panama marine barrier, a decision to recognize two species may almost be regarded as a conclusion about the world as it *is*, with workers arguing that reproductive isolation exists between two populations that have significant morphological differences. This is in contrast to a decision to recognize a pair of subspecies, a decision that could be regarded as being a shade closer to a conclusion about the world as it *might be*, with workers arguing that reproductive isolation would not be complete were gene flow once again to be possible between the two differing populations. Thus, the seemingly absolute geographic separation across Panama may unjustifiably force conclusions in favor of separate species; one can know that gene flow is now impossible, whereas it is more difficult to assume that it could take place. With more careful studies on various groups, workers may want to give increased consideration to the use of subspecies for these divergent populations, or merely to describe the morphological differences without providing names.

Crassatella marginata Keep, 1887, ex Carpenter MS

A debate has continued for many years as to whether this name was validated by Keep and about what it is. BERNARD (1983:36) has recently termed it a *nomen nudum*, dated it from 1888, and synonymized it with *Eucrassatella fluctuata*.

The name is validated in KEEP's 1887 edition (p. 179). Here is the entire entry: "*Crassatella marginata*, Cpr., Crassa-tel'-la mar-gin-a'-ta. Shells minute, about the size of large pinheads; somewhat triangular; yellowish, marked with chevrons of brown." A later version of this work (KEEP, 1904) adds that the species is "southern" (p. 50), and that it was "described in this book" (p. 281).

Although this description is sparse, and although Keep's

original specimens have not come to light in the parts of his collection now housed in the California Academy of Sciences and in the University of California at Berkeley (Barry Roth and David Lindberg, verbal communications, Jan. 1983), I think that this taxon is recognizable. There is but one genus with an internal ligament occurring in southern California that fits this description, *Halodakra*, a member of the Bernardinidae. It may be *H. salmonea* (Carpenter, 1864b), which was originally proposed in the homonymous venerid genus *Psephis* with a still more meager description (CARPENTER, 1864b:539, 611, 641; see also BERNARD, 1983:49). I am currently studying the Bernardinidae, and the relationship of *Halodakra salmonea* to the tropical eastern Pacific type species of the genus, *H. subtrigona* (CARPENTER, 1857b:82), is not yet clear. It is possible that there may be two species in southern California.

Keep initially credited his species to Carpenter, but Carpenter never proposed it. What evidently happened is this. When early collectors in southern California found some specimens of *Halodakra*, they were sent to Carpenter for identification. Perhaps forgetting all about his *Psephis salmonea*, he thought that the specimens might be another member of the Bernardinidae that he had already named from Mazatlán, *Circe margarita* CARPENTER, 1857b:81, now assigned to the genus *Bernardina* (KEEN, 1968:394, 395; fig. 4; BERNARD, 1983:49). Evidence for this comes from a label by Carpenter filed with some specimens of *Halodakra* from San Diego that had been in the Stanford University Collection (now CASIZ 036681). The label says, in part, "?*Crassatella margarita*, Cpr., Maz Cat 114. . . call it ?*Crassatella*; (not *Circe*)." Somewhere along the way to Keep, the "*margarita*" evidently was mistranscribed as "*marginata*."

Subfamily Scambulinae Chavan, 1952

Scambulinae Chavan, 1952:120

Some comments on *Crassinella*:

In my discussion of *Crassinella adamsi* Olsson, 1961 (COAN, 1979:8), I mentioned Olsson's reference to a similar, undescribed Caribbean species, which he had seen from Panama (OLSSON, 1961:183). I have not encountered any material from the Caribbean coast of Panama, but I think what Olsson may have had is *C. aduncata* WEISBORD, 1964 (pp. 197-199; 514; plt. 25, figs. 11-14), described from the Pliocene Mare Formation of Venezuela. GIBSON-SMITH & GIBSON-SMITH (1979:28) report this species from the Recent fauna of Venezuela,⁶ and I have seen specimens I tentatively assign to this species from Jamaica (LACM 74-77). It differs from the eastern Pa-

⁶ They also show that *Crassinella triquetra* WEISBORD, 1964 (pp. 199-200; 515; plt. 25, figs. 1, 2) is the same thing.

cific *C. adamsi* in attaining a larger size, having a more abrupt posterior slope, and in possessing more prominent concentric ribs. A Recent Venezuelan lot of *C. aduncata* has been placed in the California Academy of Sciences through the courtesy of Jack Gibson-Smith (CASIZ 033530).

A western Atlantic cognate of another eastern Pacific *Crassinella* has also come to my attention. It is *C. maldonadoensis* (PILSBRY, 1897:295–296) described from Uruguay, which is very similar to the eastern Pacific *C. nuculiformis* Berry, 1940. This Atlantic species has been discussed and illustrated by CASTELLANOS (1970:178–180; figs. 5–10) and by SCARABINO (1977:205, 284–285; pl. 11, fig. 2). The type specimens are in the ANSP (#70522). This species, which has been reported from Uruguay to the Golfo San Matías, Argentina, is more pointed and produced postero-ventrally and has a shorter escutcheon than *C. nuculiformis*. Its umbones are less prominent, with concentric ribs that fade out more quickly toward the ventral margin. Thanks to the courtesy of Dr. James McLean, specimens of this uncommon species have been placed in the California Academy of Sciences (CASIZ 036827).

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livr. 10—33-40; 49-56—26 May 1821
livr. 11—57-80—13 July 1821
livr. 12—41-48; 81-96—21 Sept. 1821
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Description of Five New Species of Hawaiian Eulimidae

by

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Abstract. Five new species of Hawaiian Eulimidae are described. *Trochostilifer entospinea* lives in galls in spines of *Chondrocidaris gigantea*, *T. hawaiiensis* in galls in the test of *Prionocidaris hawaiiensis*; *Vitreolina hawaiiensis* lives on the external surface of *P. hawaiiensis*, *V. chondrocidaricola* lives on and inside *Chondrocidaris gigantea*, and *Pelseneeria hawaiiensis* lives attached to the gonopores of *Aspidodiadema hawaiiensis* (all hosts Echinoidea). A second species of *Pelseneeria* is recorded, but not described, from *Stereocidaris hawaiiensis*.

INTRODUCTION

THE SPECIES OF THE family Eulimidae are almost exclusively parasitic on echinoderms and constitute a large group of gastropods in the tropical parts of the Indo-Pacific area. The species live as endo- or ecto-parasites, and many adaptations to a parasitic life are found in the group (WARÉN, in press). Comparatively few species are known from the Hawaiian Islands (KAY, 1979; WARÉN, 1980a, b, 1981), but scattered records in the literature (SCHOENBERG, 1980) and examination of museum collections show the diversity of the family to be much greater than presently known. We will here describe five new species that two of us (B.L.B. & T.A.B.) have found during offshore dredgings around the Hawaiian Islands.

The types and some additional specimens have been deposited in the U.S. National Museum, Division of Mollusks (USNM); the remaining specimens are in our collections.

Trochostilifer Warén, 1980

Type species: *Trochostilifer domus* Warén, 1980.

Remarks: Three species have previously been described in this genus. Two live in galls in the spines and one on the test of different cidaroid sea urchins (WARÉN, 1980b). The new species described below from *Chondrocidaris gigantea* was mentioned by WARÉN (1980b) but not described.

Trochostilifer entospinea

Warén, B. Burch & T. Burch, spec. nov.

(Figures 3, 4, 5, 6, 8, 21)

Type material: Holotype, one female, USNM 792378; paratype, the male from the same gall, USNM 792379.

Type locality: From a gall in a spine of *Chondrocidaris gigantea* (A. Agassiz), 10 Feb. 1980, 21°25.8'N, 157°43.3'W, 18 m, Kailua Bay, Oahu, Hawaii (1 gall with one female 2.53 mm, 1 male 1.0 mm, no egg capsules).

Material examined: One single female, 2.40 mm high, no egg capsules, 9 Dec. 1979, 21°25.8'N, 157°43.3'W, 15 m, Kailua Bay, Oahu, Hawaiian Islands, in a gall in spines of *Chondrocidaris gigantea*; 1 spine from *Chondrocidaris gigantea* with 1 gall with a female, a male and egg capsules, 1 small, empty gall (Figure 8), 13 Jan. 1980, 21°28.0'N, 157°43.0'W, 23 m, Maku manu, Oahu, Hawaiian Islands, (spine saved intact); 1 spine with 1 female, 1.56 mm, 1 male, 0.80 mm, no egg capsules, 2 spines, each with a healed gall, no cavity or snail inside, 13 Jan. 1980, 21°26'N, 157°43'W, 15 m, Mokua Rock, Oahu, Hawaiian Islands; 1 spine with a gall containing 1 female, height 3.04 mm, 1 male (crushed) and a dozen egg capsules, 3 Feb. 1980, 1 very young specimen with less than half a postlarval whorl, in a small pit beside a gall, 21°19.5'N, 158°08.4'W, 15 m, Barbers Point, Oahu,

Hawaiian Islands; 1 gall in a spine, from the type locality, serially sectioned into 10 μm sections, stained with Ehrlich's haematoxylin-eosin, containing 1 male, 1 female, several egg capsules, 1 very young specimen with less than one half postlarval whorl, found in a small pit on the outside of the same gall; 1 empty shell in shell sand, NW end of Lanai Island, Hawaiian Islands, 20°55'N, 157°03'W, 20 m, Los Angeles County Museum 74-67.

Description—Female: Shell small, grayish transparent, broadly conical with a flat base and mucronate larval shell. The larval shell (Figure 21) is 390 μm high and consists of about 3.2 distinctly convex whorls. The holotype has 3.5 slightly concave postlarval whorls with a faint shoulder just below the suture. The body whorl is abruptly rounded at the periphery and there is a well delimited basal surface. The sculpture consists of about 15 rather distinct spiral cords above the periphery and about 18 less distinct and slightly undulating spiral lines on the basal surface. There is also an axial sculpture of rather sharp incremental lines of varying strength, running all the way from the suture to the columella. The aperture is squarish with the lower part retracted rather far behind its upper parts. The outer lip is thin and very slightly flexuous (seen from the side).

Dimensions of holotype: Height of the shell 1.68 mm, maximum diameter 2.53 mm, minimum diameter 2.22 mm. (The dimensions of the aperture are irrelevant because they cannot be well defined.)

Male: Much smaller, up to 1.2 mm (approximate, specimen crushed), with up to 1.3 postlarval whorls. Its shell is more rounded and has a much less distinct sculpture than the female.

Anatomy: The quality of the fixation of the two adult specimens sectioned *in situ* in a spine did not allow any detailed examination of the anatomy, but it could be seen that the female has eyes, foot, large pedal folds, operculum and a large proboscis. The proboscis was buried in the tissues of the spine, *i.e.*, the wall of the gall. At this point the tissues of the spine had a much higher content of organic matter, judging from the higher absorption of the stain (Ehrlich's haematoxylin-eosin), than the other parts of the gall and the spine. Therefore, we assume that irritation by the parasite causes a wound-like growth zone here, which is used by the parasite. The precise way of feeding can only be determined when better fixed material is available.

Reproduction: The gall with the largest female (3.04 mm) contained about a dozen egg capsules. They are spherical, have a single, simple, smooth wall, a diameter of about 1 mm, and are attached by a short stalk. They contain 150–200 young each, in different stages of development. The diameter of uncleaved eggs is 100 μm , the height of the shell of the veliger larvae ready to hatch is 180 μm . Thus, the species has planktotrophic development because the height of newly settled larvae is 500 μm .

Remarks: The shape of the shell of *T. entospinea* resembles most closely that of *T. domus* Warén, 1980, but *T. entospinea* has a more distinctly angulated periphery than *T. domus* and also a more pronounced spiral sculpture. The other known species of *Trochostilifer* that live in galls have a much less distinct spiral sculpture and also flatter larval whorls. From *T. hawaiiensis* it can be separated by the rounder periphery and the less distinct spiral sculpture in that species.

Two spines (see material examined) had galls that evidently were in the process of healing. The outer shape and surface structure was typical for galls, but the cavity had been filled in with calcium carbonate of a slightly more spongy structure than the remaining parts of the spine. One gall contained 2 empty shells, without any visible damage, but no repair could be observed. These observations suggest that the parasite has a shorter life span than the host.

The first part of the postlarval shell in female *T. entospinea*, as in all other gall-producing species of *Trochostilifer* that have been examined, starts with about one third of a whorl which is completely smooth and quite different from the later postlarval female shell. This part of the shell is identical with that of a very young male, and may possibly indicate that the specimens pass through a more or less male phase. WARÉN (1980b) sectioned a very young solitary specimen that did not show any sexual characteristics in the anatomy. Therefore, we believe that this difference in postlarval sculpture reflects evolution from earlier protandrous hermaphroditism.

Trochostilifer hawaiiensis

Warén, B. Burch & T. Burch, spec. nov.

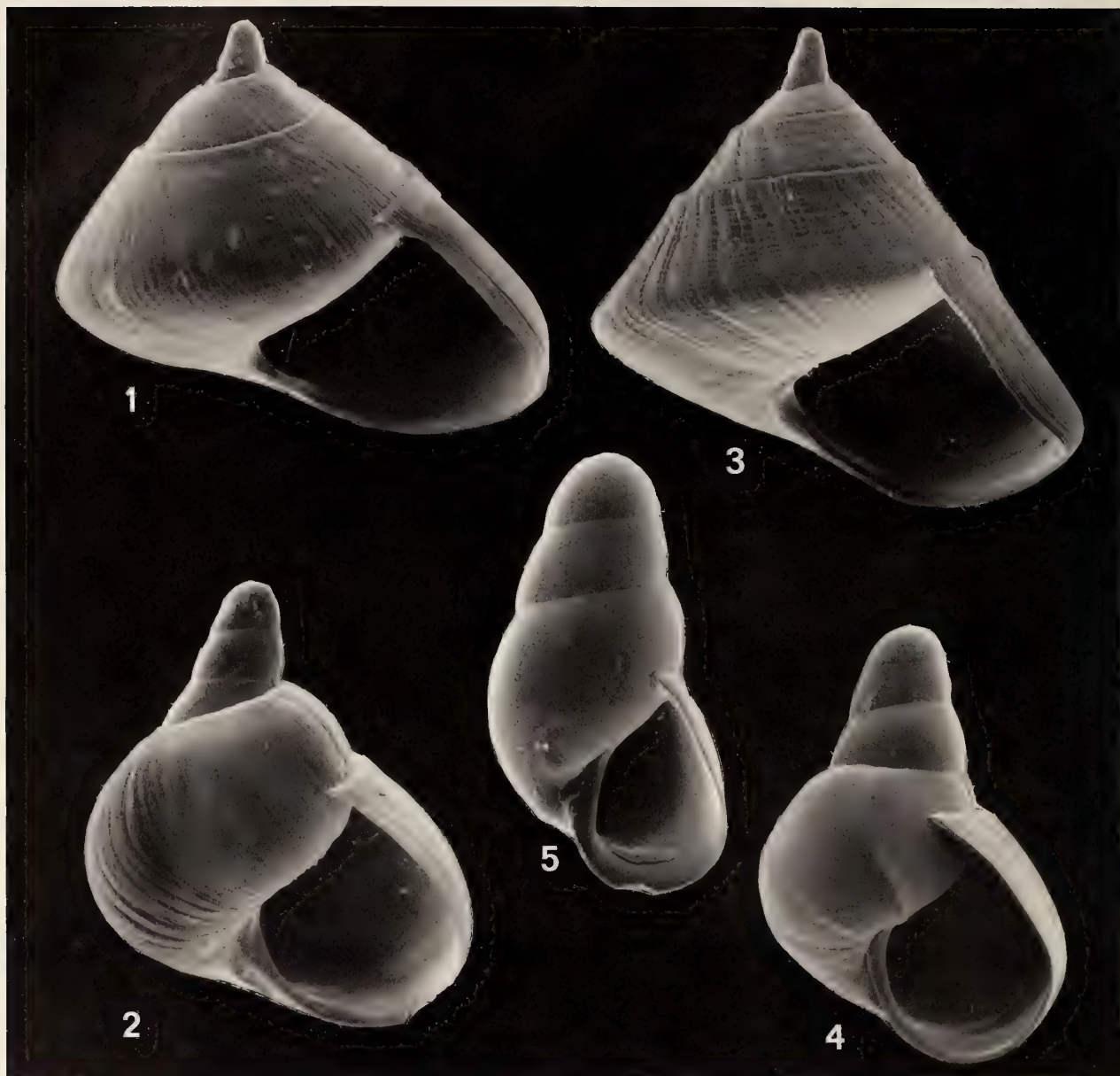
(Figures 1, 2, 7, 9, 10, 20)

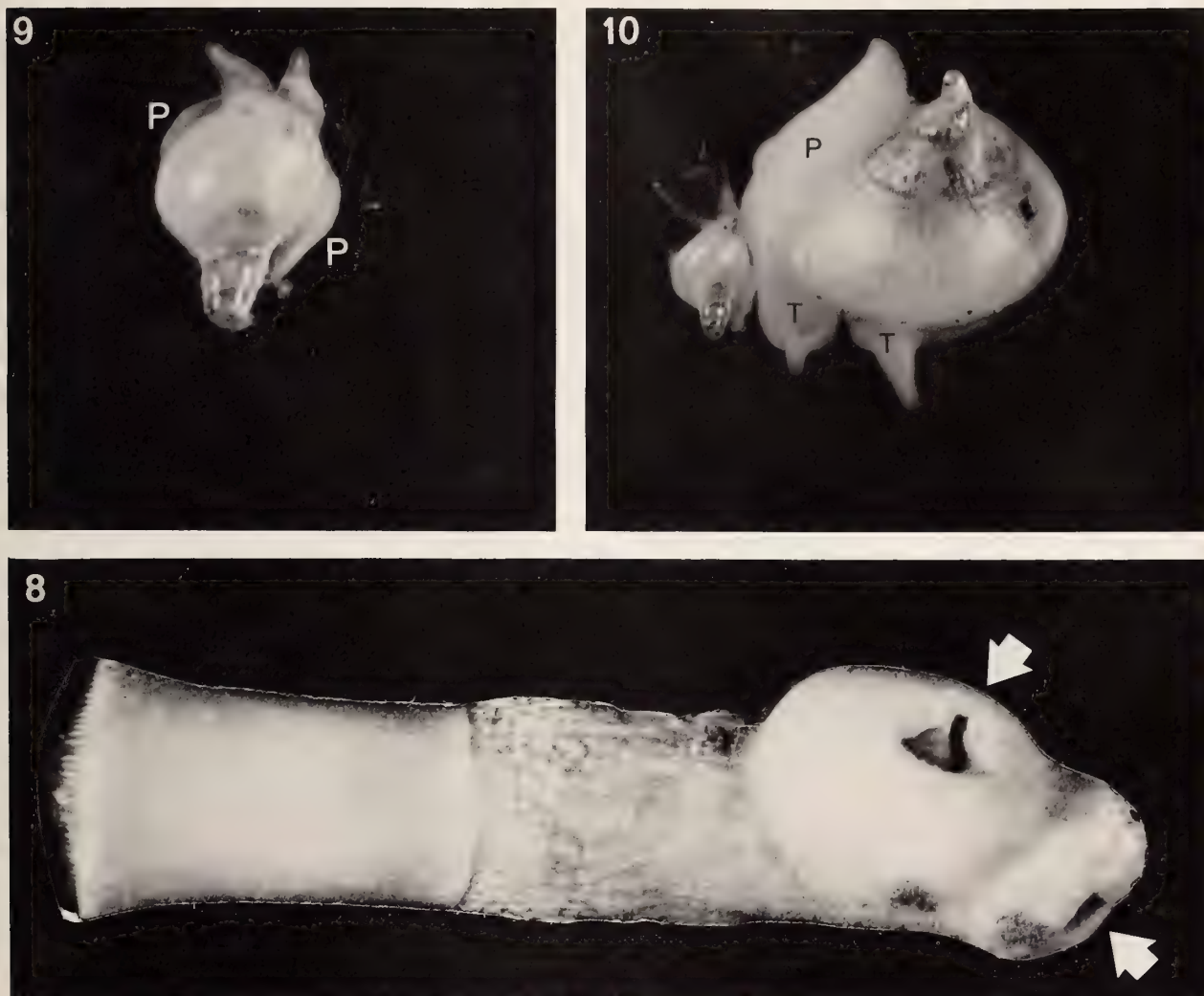
Type material: Holotype, a female, USNM 792376; paratype, a male, USNM 792377.

Type locality: From a gall in the test of *Prionocidaris hawaiiensis* (A. Agassiz), 18 Sept. 1980, 21°34.1'N, 157°49.3'W, 72 m, off Kaoio, Oahu, Hawaiian Islands.

Material examined: The type specimens, from 1 gall and: 1 female, 2.6 mm, 1 male, 1.48 mm, 17 egg capsules in another gall from the same host species and the type locality.

Description—Female: Shell small, grayish transparent, broadly conical, with a rounded base and styliform larval shell. The larval shell (Figure 20) is about 450 μm high (measured from the intersection of its outer lip and the first postlarval whorl), consists of about 3.2 almost flat whorls, and is very obliquely inserted. The holotype has a little more than 2.5 postlarval whorls, which are very slightly convex. The suture is rather deep and distinct, slightly channeled and made more distinct by the subsequent whorl joining at a right angle. The sculpture con-





Explanation of Figures 8 to 10

Figure 8. *Trochostilifer entospinea*, galls (openings indicated by arrows) in spine of *Chondrocidaris gigantea*. Total length of spine 20.5 mm.

Figure 9. Male of *T. hawaiiensis*, crawling, $\times 21$.

Figure 10. Female and male of *T. hawaiiensis*. P, pedal fold; T, tentacle. $\times 10$.

sists of distinct, sharp, close-set incremental lines of varying strength. There is also a spiral sculpture, more distinct on the basal surface, of broad but very indistinct ribs (more visible in light that shines parallel to the surface of the

shell). The periphery of the body whorl is evenly rounded, leaving the distinctly convex basal surface without any sharp demarcation. The aperture is rather rounded. Seen from the side, the outer lip is very slightly flexuous.

Explanation of Figures 1 to 7

Figure 1. *Trochostilifer hawaiiensis*. Adult female diameter 3.0 mm.

Figure 2. *T. hawaiiensis*. Adult male, height 0.86 mm.

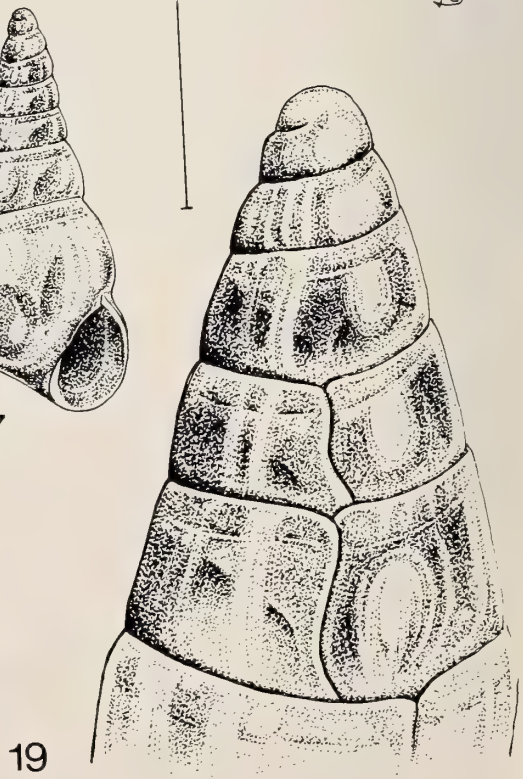
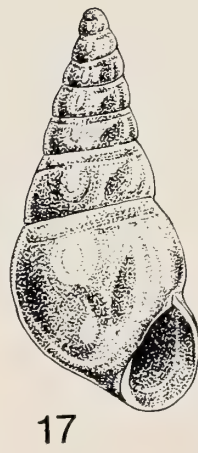
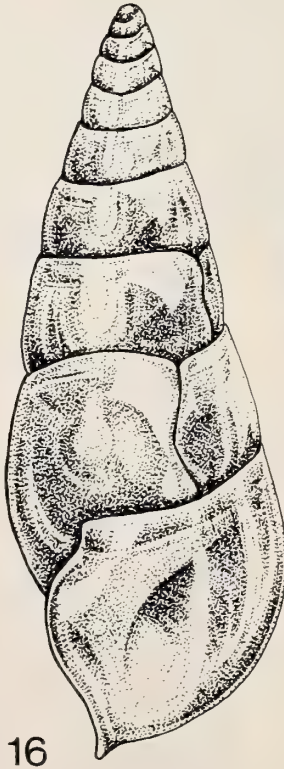
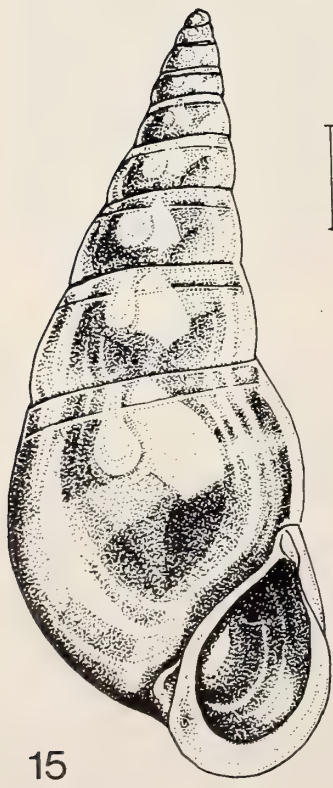
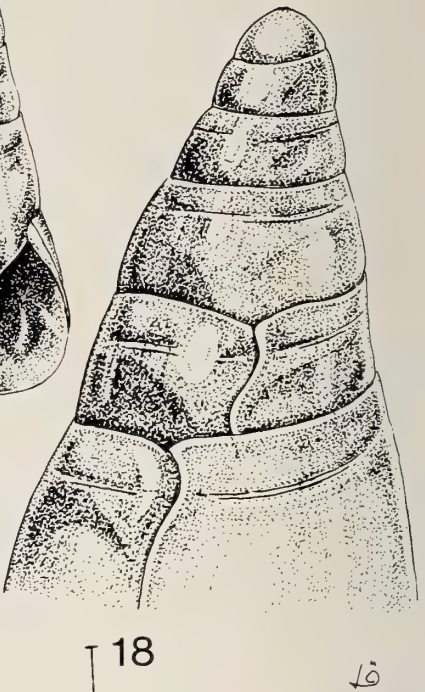
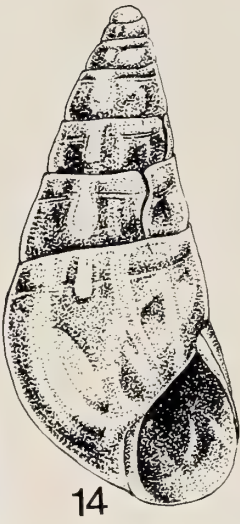
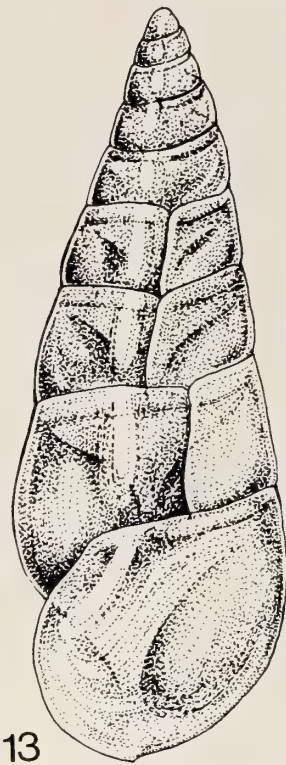
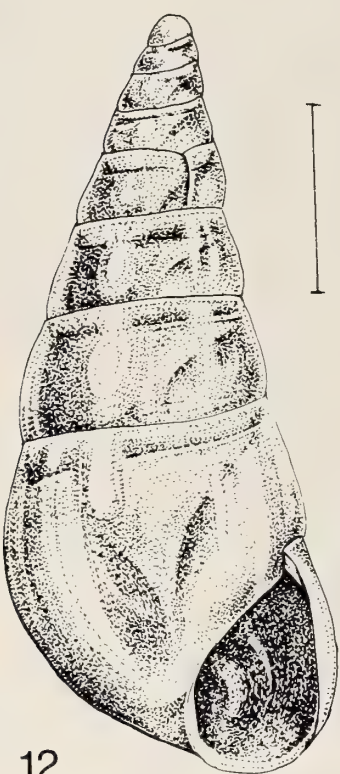
Figure 3. *T. entospinea*. Adult female, diameter 2.5 mm.

Figure 4. *T. entospinea*. Adult male, height 1.42 mm.

Figure 5. Newly settled *T. entospinea*, height 0.62 mm.

Figure 6. *T. entospinea*, apex. Scale line = 0.1 mm.

Figure 7. *T. hawaiiensis*, apex. Scale line = 0.1 mm. In Figure 6 and 7, a indicates the transition from planktotrophic to benthic life, b the change to typical female growth.



Dimensions of holotype: Height of the shell 2.30 mm, maximum diameter 2.48 mm, minimum diameter 2.12 mm.

Male: Much smaller, maximum height 1.56 mm, shell evenly rounded and almost without a trace of spiral sculpture.

Soft parts: The male (Figures 9, 10) has a functional foot, large flat, rather pointed tentacles with eyes placed centrally in their bases. One large epipodial fold from each side of the foot covers the base of the shell. Proboscis probably retractile, because it could not be seen when the male was crawling. The female (Figure 10) has flat, squarish tentacles, the tips of which very abruptly become more slender and with small, black eyes (diameter 60 μ m when preserved) centrally in the base of the tentacle. The right epipodial fold is much larger than the left. The foot is small but evidently functional and equipped with an operculum. The proboscis of living females was not observed.

Reproduction: One gall with a female of 2.6 mm height and a male contained 17 egg capsules. Each capsule has a short stalk, a smooth, simple wall and is evenly rounded with a diameter of 0.8 mm (uncleaved eggs) to 1.2 mm (veligers ready to hatch). The capsules contain about 150 eggs each. The diameter of the eggs is about 120 μ m; the height of the shell of the veligers about 180 μ m. The size of the veligers compared to the size of the larval shell clearly indicates that *T. hawaiiensis* has planktotrophic larval development.

Remarks: *T. hawaiiensis* resembles *T. mortenseni* Warén, 1980 in having a very faint spiral sculpture, but that species has flatter whorls and a suture that is less well marked than *T. hawaiiensis*.

Vitreolina Monterosato, 1884

Type species: *Eulima incurva* Renieri in Bucquoy, Dautzenberg & Dollfus, 1883, subsequent designation, Bucquoy, Dautzenberg & Dollfus, 1898.

Remarks: The type species is probably a parasite of some ophiuroids, and originates from the Mediterranean. We are convinced that the two species described below do not belong to *Vitreolina* but should be classified in a new genus; lack of soft parts has made us hesitate to describe a

new genus for them. We have, therefore, placed them in *Vitreolina* provisionally, because of some similarity in shell characters.

Vitreolina hawaiiensis

Warén, B. Burch & T. Burch, spec. nov.

(Figures 15, 16, 17, 19)

Type material: Holotype (a female) USNM 792381 and a paratype (a male) USNM 792382.

Type locality: Found on *Prionocidaris hawaiiensis*, 18 Sept. 1980, 21°34.1'N, 157°49.3'W, 72 m, off Kaoio, Oahu, Hawaiian Islands.

Material examined: The type material and: 1 female, 2.20 mm, from *Prionocidaris hawaiiensis*, 8 Sept. 1980, 21°33.5'N, 157°49.0'W, 72 m.

Description—Female: Shell small, conical, slightly curved, vitreous and slender, with numerous, slowly increasing whorls. The larval shell consists of a little more than 3 whorls and its height is 450 μ m. Its whorls are colorless, perfectly transparent, and very slightly convex. The holotype has 5.5 postlarval whorls which are almost flat, except for the body whorl which is quite inflated. The suture is very indistinct and the false suture (the line marking the internal connection of the whorls) is much more conspicuous. There are 4 incremental scars after the one that marks the connection of the larval and postlarval shells, placed slightly more than one whorl apart. The last of these scars marks the point where the whorls become inflated. The aperture is low and rounded, distinctly broader in its lower part. Seen from the front, the outer lip is slightly flexuous; seen from the side it is retracted at the suture, strongly projecting below this, then retracted again, in its lower part. The most projecting part is situated just above the upper third.

Dimensions of holotype: Height of the shell 3.48 mm, diameter 1.40 mm, height of the aperture 1.04 mm, breadth 0.60 mm.

Male: Shell smaller (1.8 mm high), body whorl not inflated.

Soft parts: Not studied, but the general coloration of the live animal is evenly yellowish to reddish brown.

Explanation of Figures 12 to 19

Figures 12, 13. *Vitreolina chondrocidaricola*, female.

Figure 14. *V. chondrocidaricola*, male, drawn at the same scale.

Figures 15, 16. *V. hawaiiensis*, female.

Figure 17. *V. hawaiiensis*, male, drawn at the same scale.

Figure 18. *V. chondrocidaricola*, apex.

Figure 19. *V. hawaiiensis*, apex. The uppermost labial scars in Figures 18 and 19 mark the change from planktonic to benthic life.

Scale lines: Figures 12 to 17, 0.5 mm; Figures 18 to 19, 0.25 mm.

Remarks: The specimens were found on the spines and test of the host. The precise nature of the parasitism is not known and because of the small number of specimens, we did not want to break a shell to examine the soft parts.

Vitreolina chondrocidaricola

Warén, B. Burch & T. Burch, spec. nov.

(Figures 12, 13, 14, 18)

Type material: Holotype (a female) USNM 792383 and 8 paratypes USNM 792384.

Type locality: From the intestine of *Chondrocidaris gigantea*, 9 Dec. 1979, 21°25.8'N, 157°43.3'W, 15 m, Kailua Bay, Oahu, Hawaiian Islands.

Material examined: The type material and: 3 specimens, from spines of *C. gigantea*, 13 Jan. 1980, 21°28.0'N, 157°43.0'W, 23 m, Maku Manu, Oahu, Hawaiian Islands, USNM 792385; 2 specimens from dorsal spines of *C. gigantea*, 3 Feb. 1980, 21°20.5'N, 158°08'W, 23 m, Kahe Point, Oahu, Hawaiian Islands, USNM 792386; 39 specimens from spines, 6 young and crushed specimens from coelomic cavity of *C. gigantea*, 10 Feb. 1980, 21°25.8'N, 157°43.3'W, 18 m, Kailua Bay, Oahu, Hawaiian Islands; 8 specimens from dorsal spines of *C. gigantea*, 9 March 1980, Pilokahe Point, Oahu, Hawaiian Islands, 18 m, USNM 792387.

Description—Female: Shell small, colorless, transparent, rather broadly conical, straight or slightly curved. The larval shell consists of about 4 slightly convex, colorless whorls with a distinct suture. The height is about 480 μ m. The holotype has 4 postlarval whorls, which are less convex than the larval whorls, perfectly smooth and with a false suture more distinct than the real suture which is shallow and inconspicuous. There are 3 incremental scars in the holotype, at intervals of a little more than 1.0 whorls. The aperture is low and rounded, deeply excavated in its lower part. The outer lip is retracted at the suture and evenly curved and projecting below this with its most protruding part situated at the midpoint of its height (seen from the side).

Dimensions of holotype: Height of the shell 2.10 mm, diameter 0.86 mm, height of the aperture 0.64 mm, breadth 0.40 mm.

Male: Half the size of the female and with correspondingly fewer whorls.

Soft parts: Not studied, but from a photograph it can be seen that the animal has rather long, cylindrical tentacles with black eyes at the base, a functional, small and short foot, and patchy, brownish pigmentation.

Remarks: *V. chondrocidaricola* can be separated from *V. hawaiiensis* by its less projecting outer lip and less inflated body whorl.

There are a few species of eulimids known that resem-

ble the two species of *Vitreolina* described here, but no Indo-Pacific ones. The small size, pointed larval shell, and low, rounded aperture make them easily distinguishable from other eulimids. Another helpful detail is the suture, which is distinctly curved just in front of, and after, the incremental scars.

Pelseneeria Koehler & Vaney, 1908

Type species: *Pelseneeria profunda* Koehler & Vaney, 1908, subsequent designation Winckworth, 1932.

Remarks: The species of *Pelseneeria* are ectoparasites on regular sea urchins. Most of them crawl around on the test, presumably feeding on the epithelium or introducing the proboscis into the tube feet to suck body fluid. One previously known species (SCHEPMAN & NIERSTRASZ, 1909, as *Stilifer* sp.), from *Aspidodiadema tonsum* A. Agassiz, is known to be permanently attached, with its proboscis introduced into a gonad of the host.

Pelseneeria sp.

In the collections of the Division of Mollusks, USNM, there is a pair of specimens of *Pelseneeria*, from U.S. Fisheries Commission (USFC) "Albatross" Station 4044, 1902, off Kawaihae Light, W coast of Hawaii, 356–520 m.

The shells have been completely dissolved by acidic alcohol, but the soft parts seem to be well preserved. Nothing is mentioned about hosts. In AGASSIZ & CLARK's (1908) report on the Echinoidea from these dredgings, there is mentioned only a single species of echinoid from the station mentioned above, viz. *Stereocidaris grandis* (Döderlein). MORTENSEN (1928:22–23) disagreed with this identification and regarded this specimen as a distinct species, *Stereocidaris hawaiiensis* Mortensen, 1928. He also mentioned that the specimen in question had gastropod egg capsules attached at the periproct. The specimen is still in the collections of the Division of Echinoderms, USNM 27334. Examination of the specimen revealed 9 egg capsules attached to the test, but no enlarged gonopores were noticed, although the dorsal part of the test was cleaned of spines. It can, therefore, be assumed that these two specimens represent a second Hawaiian species of *Pelseneeria*, parasitic on *Stereocidaris hawaiiensis*, in addition to *P. hawaiiensis*. We will, however, not name it here, because the absence of the shell would complicate future identification.

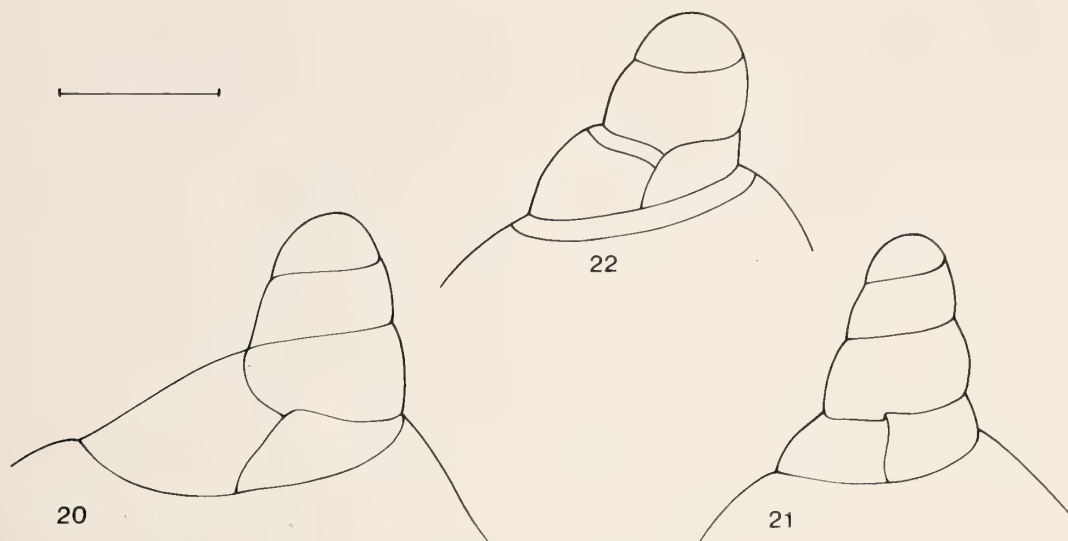
Pelseneeria hawaiiensis

Warén, B. Burch & T. Burch, spec. nov.

(Figures 22, 25, 26)

Type material: Holotype USNM 111067 and 2 paratypes, USNM 792380.

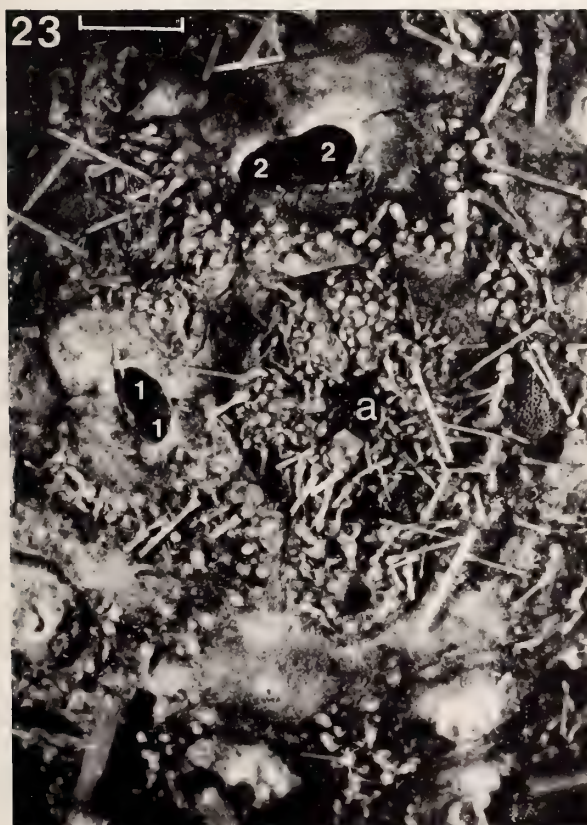
Type locality: Attached by the proboscis (which is introduced through the gonopore) on a specimen of *Aspidodi-*



Explanation of Figures 20 to 22

Figures 20 to 22. Apices. Figure 20. *Trochostilifer hawaiiensis*.

Figure 21. *T. entospinea*. Figure 22. *Pelseneeria hawaiiensis*.
Scale line = 0.25 mm.



Explanation of Figures 23 and 24

Figure 23. Aboral part of *Aspidodiadema hawaiiense* (USNM 111067) with holes from proboscides of *Pelseneeria hawaiiensis*. a, anus of the sea urchin; 1,1 and 2,2 show the positions of the



individual proboscides of the two pairs of parasitic snails. Scale line = 2 mm.

Figure 24. *Pelseneeria hawaiiensis*, holotype, 5.64 mm high.

adema hawaiiensis (Mortensen), USFC "Albatross" Station 3865, Pailolo Channel, Hawaiian Islands, 500 m.

Material examined: The type material and: 2 specimens, 5.04 and 2.40 mm high, attached as above, on *Aspidodiadema hawaiiensis*, 11 Nov. 1979, 21°14.4'N, 157°56.6'W, 470 m, Mamala Bay, Oahu, Hawaiian Islands; (4 specimens reported by AGASSIZ & CLARK (1908), USFC "Albatross" Station 3839, off Lae-o, Ka Laau Light, Molokai, Hawaiian Islands, 570–580 m and their host were examined, but only fragments remained).

Description: Shell yellowish to brownish, rather thin and fragile, rather broadly conical, with a blunt mucronate larval shell. The larval shell (Figure 22) consists of about 2 slightly convex whorls and its axis forms a distinct angle with that of the postlarval whorls. The holotype has 4.0 postlarval whorls, sculptured with faint incremental lines and 3 irregularly placed and indistinct incremental scars. The whorls are slightly convex and the suture is shallow but distinct. The subsutural zone occupies about $\frac{1}{2}$ of the height of the whorls. The periphery of the whorls is more angulated than rounded, which gives the base of the shell a rather flat appearance. The aperture is rather large and evenly rounded in its lower part. The columella is thin and the parietal wall is not covered by a callus.

Dimensions of holotype: Height of the shell 5.64 mm, diameter 3.40 mm. Height of the aperture 2.47 mm.

Soft parts: Typical for *Pelseneeria*, but eyes are lacking. The specimens did not leave the host when disturbed, but had to be pulled off the host. The animal is unpigmented. The proboscis is introduced through the gonopore which becomes enlarged (cf. Figure 23). The part of the proboscis which is inside the gonad is greatly enlarged by being filled with and inflated by the body-fluid of the parasite, thereby probably functioning as an anchor and keeping the snail in position on the host. The damage of the gonopore also indicates that the snail is permanently attached to the same gonopore.

Remarks: SCHEPMAN & NIERSTRASZ (1909) never named "*Stilifer* sp." from *Aspidodiadema tonsum* because the shell was broken. It is, therefore, not possible to say whether their specimen belonged to a different species. The mode of parasitism, being attached to the gonopores, distinguishes their species and *P. hawaiiensis* from all other known species of *Pelseneeria*.

All specimens examined occurred in pairs, presumably to ensure contact for copulation.

The present species was first reported on by AGASSIZ

& CLARK (1908) in their treatment of the echinoids taken by the USFC in Hawaii. They had found four specimens on one host (of which one pair can be seen on their plate 58, fig. 7), determined *Aspidodiadema meijeri* A. Agassiz & Clark (sic; the correct author is Döderlein). MORTENSEN (1939), however, after having examined their specimens regarded them as a distinct species and described it as *Aspidodiadema hawaiiensis* Mortensen, 1939.

AGASSIZ & CLARK (1908) noticed that the genital plates on which the snails were attached had more numerous spines than the other genital plates. Their observation was based on two parasitized genital plates; but, if this tendency is persistent, the modification is certainly adaptive for the parasite, giving better protection from grazing fishes.

ACKNOWLEDGMENTS

We want to direct our thanks to the Divisions of Mollusks and Echinoderms, USNM, for examination of material of hosts and parasites and for preparation of the SEM photos of *Trochostilifer*. Warén's work has been supported by grants from the Swedish Natural Science Research Council.

We also want to thank Mr. Keith Zeilinger, who collected the specimens of *Chondrocidaris*.

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A New Species of *Ischnochiton* (Mollusca: Polyplacophora) in the Gulf of California

by

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Abstract. A new species of chiton, *Ischnochiton carolianus* Ferreira, spec. nov., is described from San Carlos, Sonora (type locality) and Smith Island, Bahía de los Angeles, Gulf of California, Mexico, dredged at depths of 61-91 m to 182 m. Specimens are very small (up to 8.5 mm long) resembling *I. tenuisculptus* (Carpenter, 1864).

ALMOST SIMULTANEOUSLY, I was entrusted with two collections of chitons from the Gulf of California, independently obtained by Carol and Paul Skoglund, Phoenix, Arizona, and Forrest and Leroy Poorman, Westminster, California. As fortune would have it, both collections contained specimens of a species which further study revealed to be new to science.

Class Polyplacophora Gray, 1821

Order Neoloricata Bergenhayn, 1955

Suborder Ischnochitonina Bergenhayn, 1930

Family Ischnochitonidae Dall, 1889

Genus *Ischnochiton* Gray, 1847

Ischnochiton carolianus Ferreira, spec. nov.

(Figures 1 to 6)

Diagnosis: Very small (largest specimen, 8.5 mm long) chitons, carinate, not beaked. Lateral areas well defined with small, convex, round, granules in quincunx; central areas pitted in quincunx; mucro anterior. Girdle with very small, imbricated scales, with 10-12 riblets. Radula with unicuspid major lateral teeth.

Type material: **Holotype** and 11 **paratypes**, dredged at 100 m, 5 km south of San Antonio Pt., San Carlos, Guaymas, Sonora, Mexico, *leg.* Forrest and Leroy Poorman, November 1980; and 3 **paratypes**, dredged at 61-91 m, 5 km south of Tetás de Cabras, San Carlos, Sonora, Mex-

ico, *leg.* Carol and Paul Skoglund, November 1979. **Holotype** deposited at the California Academy of Sciences (CAS 035074); **paratypes**, at the California Academy of Sciences (CAS 035075), Los Angeles County Museum of Natural History (LACM 2032), United States National Museum of Natural History (USNM 749857), Academy of Natural Sciences of Philadelphia (ANSP 357502) and in the private collections of Carol and Paul Skoglund, Forrest and Leroy H. Poorman, and Antonio J. Ferreira.

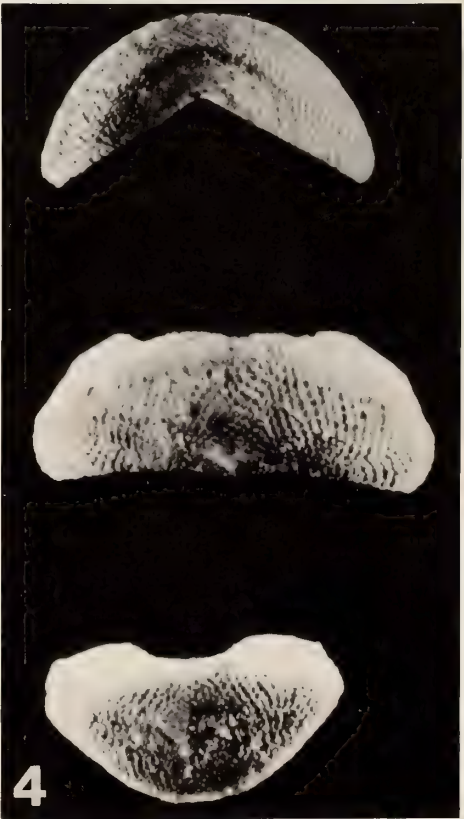
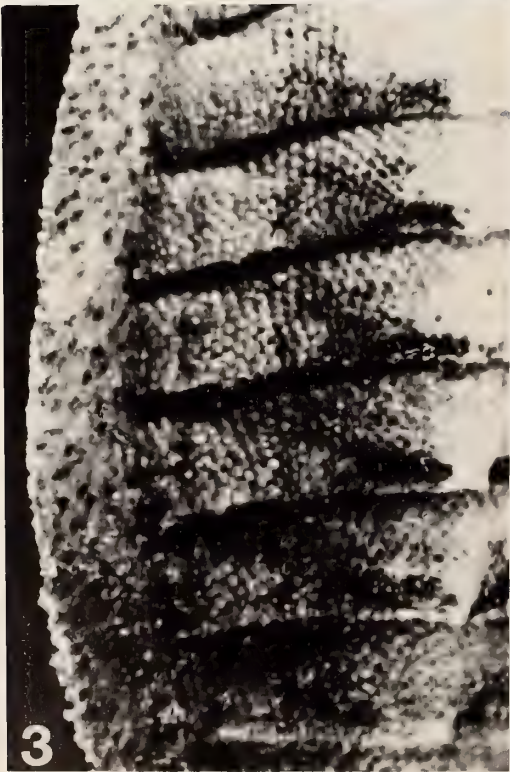
Other material: Smith Id. (north end), Bahía de los Angeles, Gulf of California, Mexico, 3 specimens dredged at 182 m, *leg.* Carol and Paul Skoglund, May 1980.

Type locality: 5 km south of Punta San Antonio, San Carlos, Sonora, Mexico (27°56'N; 111°06'W).

Description: **Holotype** (Figures 1, 2, 3)—dry specimen, 7.5 mm long, 4.5 mm wide, uniformly brown with some irregular black smudges (? artifact) on valves and girdle scales; valves moderately elevated and carinate; posterior edge of intermediate valves, straight, not (or obsoletely) beaked; lateral areas well defined, moderately elevated; anterior valve, lateral areas of intermediate valves, and postmucro area of posterior valve sculptured with inconspicuous, round, convex granules, about 80 μ m in diameter, close together in quincunx; central areas minutely punctated in quincunx; mucro anterior, inconspicuous; postmucro, concave; girdle, 0.6 mm wide at valve iv, uniformly covered with very small, oval, imbricated scales; gills unascertainable.

Paratypes—in several shades of brown (one mottled with reddish hues), agreeing with holotype in all major respects. Size range, including girdle, 8.5 \times 5.4 mm to

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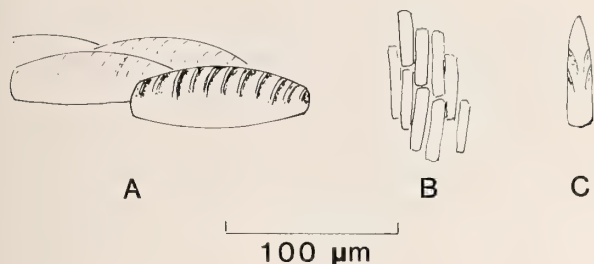


Figure 5

Ischnochiton carolianus Ferreira, spec. nov. **Paratype** (CAS 035075); dry specimen, 6.0 mm long, including girdle. Girdle elements: A. scales of upper surface; B. scales of undersurface; C. spicules of margin.

3.8 × 2.5 mm; body width/length, mean = 0.65 (SD = 0.35; N = 11).

Paratype (Figure 4), 6.0 × 4.0 mm, disarticulated: anterior valve, 1.0 mm long, 2.1 mm wide; posterior valve, 1.2 mm long, 2.2 mm wide, width of sutural laminae/width of sinus = 0.4. Articulamentum white; sutural laminae subrectangular, very short (0.2 mm long on valve viii), almost continuous across a very shallow and poorly defined sinus; insertion teeth sharp, small; slits 12-1-8 followed by slit-rays. Girdle's upper surface covered with strongly imbricated, oval scales (Figure 5A), up to 100 μm long, with 10-12 riblets; undersurface with transparent, rectangular scales (Figure 5B), 50 × 20 μm; marginal fringe of inconspicuous spicules (Figure 5C), 60 × 30 μm, with oblique, screw-like striations. Radula, 2.0 mm long, comprising 24 rows of mature teeth; median tooth about 120 μm long, edges slightly incurved, 40 μm wide at anterior blade, 30 μm at waist; first lateral teeth, 50 μm long, with small knob at antero-outer corner (Figure 6A); major lateral teeth with unicuspid head (Figure 6B); outer marginal teeth 65 μm long, 45 μm wide.

Distribution: *Ischnochiton carolianus* is known only from the type locality, San Carlos, Sonora, Mexico, and Smith Id., Bahía de los Angeles, Gulf of California, Mexico, at depths of 61-91 m to 182 m.

Remarks: *Ischnochiton carolianus* resembles *I. tenuisculptus* (Carpenter, 1864), a species occurring from Panama to Peru, in color, shape of body, and the simplicity of

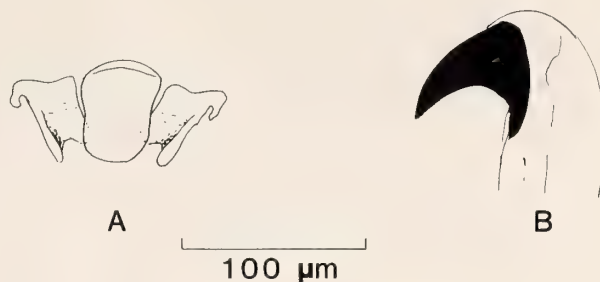


Figure 6

Ischnochiton carolianus Ferreira, spec. nov. **Paratype** (CAS 035075); dry specimen, 6.0 mm long, including girdle. Radula: A. median and first lateral teeth; B. head of second (major) lateral tooth.

tegmental features. The two species seem to differ in size (largest specimen examined of *carolianus*, 8.5 mm long; of *tenuisculptus*, 15.8 mm long), and are quite distinct in the (1) tegmental granules of lateral areas and end valves (regular in size and height in *carolianus*; larger and higher round granules, standing out, randomly, amidst smaller and lower ones in *tenuisculptus*); (2) mucro (definitely anterior in *carolianus*; central or only slightly anterior in *tenuisculptus*); (3) girdle scales (up to 100 μm long in *carolianus*; up to 180 μm long in *tenuisculptus*); and (4) radula's major lateral teeth (unicuspid in *carolianus*; bicuspid in *tenuisculptus*).

The species is here called *carolianus* after Carol Skoglund, Phoenix, Arizona, who, together with her husband Paul E. Skoglund, first collected and made available specimens for study.

ACKNOWLEDGMENTS

Appreciation is here expressed to Carol and Paul E. Skoglund and to Forrest L. and Leroy H. Poorman, who provided the material for study; and to Dr. Barry Roth, California Academy of Sciences, who critically reviewed the manuscript.

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Explanation of Figures 1 to 4

Figure 1. *Ischnochiton carolianus* Ferreira, spec. nov. **Holotype** (CAS 035074); dry specimen, 7.5 mm long, including girdle.

Figure 2. Same as in Figure 1. Side view.

Figure 3. Same as in Figure 1. Close-up of lateral and pleural areas.

Figure 4. *Ischnochiton carolianus* Ferreira, spec. nov. **Paratype** (CAS 035075); dry specimen, 6.0 mm long, including girdle. Tegmental side of valves i, vi, and viii.

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Records of *Cuthona pustulata* (Alder & Hancock, 1854) from the Canadian Pacific

by

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Abstract. A tergipedid nudibranch found in the shallow subtidal waters of British Columbia, Canada, differs from all known sympatric species. Specimens closely resemble the descriptions of *Cuthona pustulata* (Alder & Hancock, 1854) previously known only from the northeastern Atlantic. The morphology of this species in both the northeastern Pacific and northeastern Atlantic is compared. Closely related and sympatric species are discussed.

INTRODUCTION

A TERGIPEDID nudibranch first collected at Saltspring Island, Strait of Georgia, British Columbia, Canada, in May 1977, differed substantially from the four known sympatric tergipedid species (*Catriona columbiana* [O'Donoghue, 1922], *Cuthona albocrusta* [MacFarland, 1966], *C. concinna* [Alder & Hancock, 1843] and *C. divae* [Marcus, 1961]). This species, identified as *Cuthona pustulata* (Alder & Hancock, 1854) has been previously recorded from the northeastern Atlantic. Its presence in the northeastern Pacific represents a significant addition to its known range.

The genus *Cuthona* has been enlarged considerably, particularly in recent years. *Trinchesia*, *Xenocratena*, *Catriona*, *Njurja*, *Narraeolidia*, *Toorna*, and *Selva* are presently considered junior synonyms by MILLER (1977). The inclusion of the genus *Catriona*, however, has been disputed by GOSLINER & GRIFFITHS (1981). WILLIAMS & GOSLINER (1979) added *Precuthona*, as the type species *Precuthona peachi* (Alder & Hancock, 1848) appears to be a junior synonym of the type species of *Cuthona*, *Cuthona nana* (Alder & Hancock, 1842). GOSLINER (1981) also included *Subcuthona*, making a total of over 80 species

in this genus. *Cuthona* species are listed primarily in MARCUS (1958), SCHMEKEL (1968), BURN (1973), and WILLIAMS & GOSLINER (1979). BROWN (1980) redescribed British species including the type species *Cuthona nana*.

MATERIAL

On May 1, 1977, the first two specimens of *Cuthona pustulata* were collected by S. Millen, 15 m below Canadian datum at Musgrave Landing, Saltspring Island, British Columbia (latitude 48°48'N; longitude 123°32'W). On April 18, 1980, an additional eight specimens were collected from *Halecium* sp. by R. Long diving at 12 m in the same area.

At Porlier Pass, Galiano Island, British Columbia (latitude 49°01'N; longitude 123°36'W) on April 29, 1979, two specimens were collected by S. Millen on *Halecium* sp. at a depth of 10 m. A dive at this site by S. Millen on May 2, 1982, yielded 33 specimens and spawn on *Halecium* sp. at depths of 14-18 m. Seven voucher specimens have been deposited in the British Columbia Provincial Museum, BCPM 983.26.1, and six voucher specimens in the California Academy of Sciences, CASIZ 031673.

DESCRIPTION

The body is slender (Figure 1) and up to 20 mm in length. Body color is translucent white with opaque white ovo-

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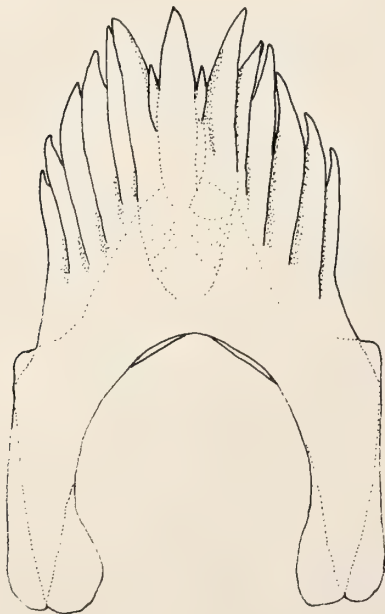
Figure 1

Cuthona pustulata, 16 mm in length. Drawn from a color transparency taken by Ron Long.

testis and brown jaws visible through the skin. The oral tentacles are cylindrical with blunt tips. They arise from the antero-lateral corners of the head and are flecked on the dorsal surface with opaque white spots. The rhinophores are smooth and slightly longer than the oral tentacles. They arise close to each other. Fine, opaque white spots decorate the rhinophores except near their bases. The head is globular with a T-shaped mouth opening.

The cerata are elongate and cylindrical, with rounded tips containing small, white cnidosacs. The liver divertic-

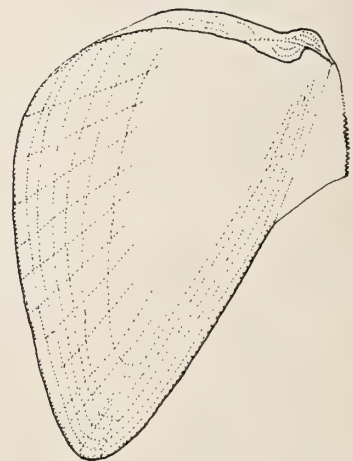
ula are dark reddish brown and granular. The ceratal sheath is transparent. Above the cnidosacs, the ceratal tips are clear. Each bears a faint, opaque white subapical band. There are small opaque white flecks on the distal halves of the cerata, and two or three large white spots on the proximal halves. The cerata are arranged in 8 to 14 rows. An example of the ceratal arrangement of a typical 16-mm specimen (live length) is 2,4,6,7,8; 6,6,5,4,4,3 on the right and 3,4,6,5,7; 6,6,4,4,3,2 on the left (using the counting method of EDMUNDS, 1970). The pre-cardiac rows are opposite; the post-cardiac rows are slightly anterior on the left side. The anus is posterior in the inter-hepatic space, just below the cardiac hump, with the renal pore directly ahead of it. The gonopore is below the second or third ceratal row of the right anterior liver branch.



20 μ m

Figure 2

Radular tooth drawn from a SEM micrograph.



1 mm

Figure 3

Jaw with a single row of denticles on the masticatory margin.

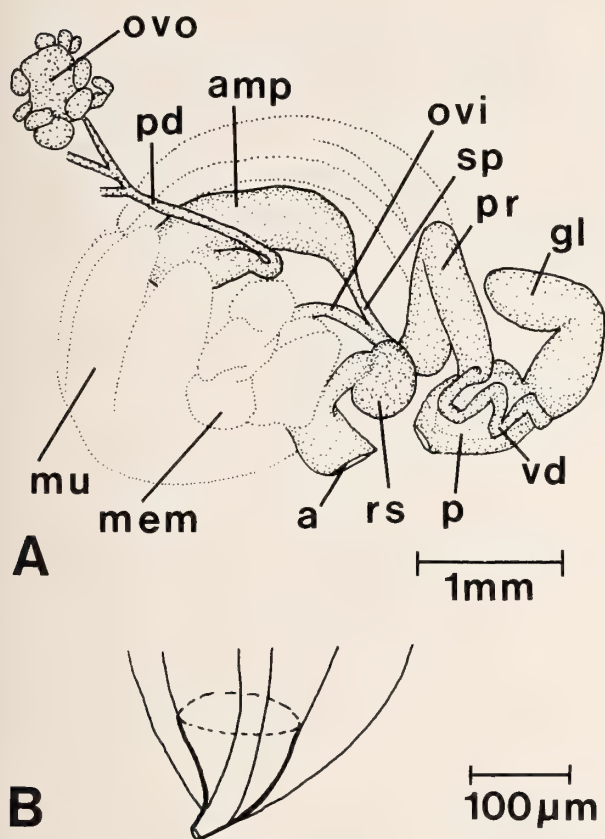


Figure 4

A. *Cuthona pustulata* reproductive system from a camera lucida drawing. Key: a, female aperture; amp, ampulla; gl, penial gland; mem, membrane gland; mu, mucous gland; ovi, oviduct; ovo, ovotestis; p, penis in sac; pd, preampullary duct; pr, prostate; rs, receptaculum seminis; sp, spermoviduct; vd, vas deferens. B. Penial tip showing stylet and vas deferens.

The foot is rounded anteriorly with a thickened anterior margin and a small flange. The long, pointed tail has an irregular line of opaque white spots.

The uniseriate radula contains 12 to 26 teeth. The central cusp is slightly shorter or equal in length to the first of the five to six laterals on each side (Figure 2). There is sometimes a small intermediate denticle on each side of the central cusp. The thin, triangular jaws (Figure 3) have a well developed masticatory margin with approximately 16 fine denticulations.

In the reproductive system (Figure 4) the ovotestis is connected by the preampullary duct to a small U-shaped ampulla. The postampullary duct branches to form an oviduct entering the female gland mass and a vas deferens enlarged into a prostatic portion. The more distal, non-prostatic portion of the vas deferens enters the penial sac at the junction of the large, unstalked, penial gland. The penis has a short, conical, 44–125 µm long, stylet (Figure

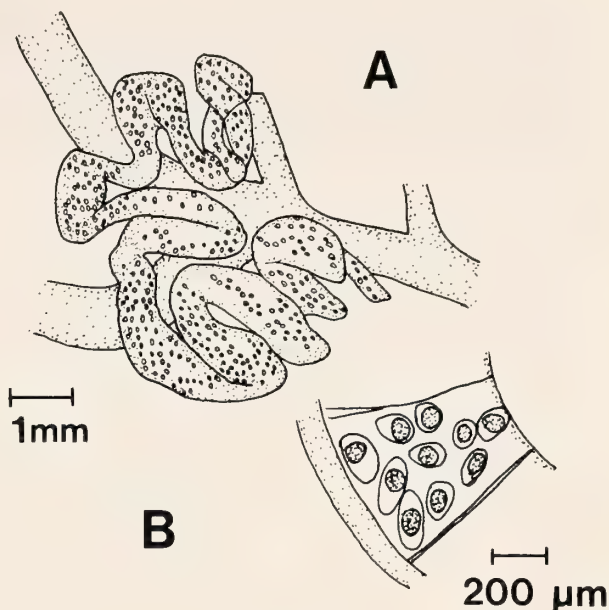


Figure 5

A. Egg mass of *Cuthona pustulata* laid on the hydroid *Halecium* sp. B. Close-up of the egg mass showing the single eggs and large capsules.

4B). There is a round, stalked receptaculum seminis near the separate, female aperture.

Spawning was observed in two different years in early May. The eggs (Figure 5) are laid on the shafts of *Halecium* sp., towards the center of these hydroid colonies, in concealed locations. The spawn ribbon, a white, convoluted coil attached by a small membrane, forms a sausage-shaped mass. The oval egg capsules are much larger than the eggs (Figure 5B). One egg 120 µm in diameter is typical for each capsule, but occasionally there are two or three.

After 18 to 19 days at 10°C, the eggs hatched into planktotrophic veligers with Type 2 shells of THOMPSON (1961). The veligers developed eyes after three days and appeared competent by two weeks. Shortly after hatching the digestive gland turned green, an indication that the larvae were feeding. Metamorphosis did not take place and the veligers died after three weeks.

HABITAT

Animals were found subtidally on the hydroid *Halecium* sp. on rocky bottoms, 10 to 18 m below Canadian datum, in April or early May. In two different years the collection localities were rechecked unsuccessfully in June. Apparently the period of peak abundance is short.

DISCUSSION

Most *Cuthona* species vary considerably in coloration but have colors other than white on their notum, cerata, oral

Table 1
Cuthona pustulata from Britain and the northeastern Pacific.

Locality	Britain (from BROWN, 1980)	Northeastern Pacific		
Max. live length	18 mm	20 mm		
Preserved length	8 & 11 mm	2 mm	7 mm	12 mm
No. ceratal rows	12	8	11	14
No. precardiac rows	6	3	5	6
Max. no. cerata	126	52	105	230
Max. no. cerata/row	8	5	7	15
Color:				
Ceratal epidermis	large white spots	large white spots		
Ceratal cores	lt. brown/pink/yellow	reddish brown		
Tentacles	white patches	white patches		
Rhinophores	white patches	white patches		
No. radular teeth	15-24	12-26		
No. tooth denticles	4-7/side; central shorter	5-9/side; central shorter or equal		
Jaw margin	finely denticulated	13-16 fine denticles		
Penial gland	base of vas deferens	base of vas deferens		
Penial armature	conical stylet	conical stylet		
Vas deferens	prostatic portion	prostatic portion		
Seminal receptacle	near female opening	near female opening		
Spawn mass	white, small coils	white, one convoluted coil		
No. eggs	approx. 700/spawn mass	approx. 450/spawn mass		
Egg size	180 μ m	120 μ m		
Larvae	? non-pelagic	planktotrophic; shell Type 2		

tentacles, or rhinophores. The large, distinctive, white spots on the cerata of our specimens, and absence of any other colors, were characteristics shared only by *C. fulgens* (MacFarland, 1966), *C. perca* (Marcus, 1958), and *C. pustulata* (Alder & Hancock, 1854).

Cuthona fulgens differs from our specimens in that the hepatic lobes of the cerata have a lemon-yellow band at their bases and below the cnidosacs. In addition, the radula of *C. fulgens* has a much larger number of teeth (59 compared to a maximum of 26 in our specimens), and its receptaculum seminis is located on a longer stalk, more distally positioned with respect to the female aperture.

Cuthona perca sometimes has olive-green flecks and a light orange head. When these are absent it nevertheless differs from our specimens in having olive-green to brownish digestive gland tissue in the cerata and notum. The radula has more teeth (35) with more denticles (up to 11 on each side of the central cusp). The rhinophores and oral tentacles of *C. perca* are shorter. It has a larger, more distinct inter-hepatic space and a longer tail. The spawn of *C. perca* is saccate, not coiled like that of our specimens. Lastly, *C. perca* has been observed to feed on anemones, not hydroids (GOSLINER, 1980).

Cuthona pustulata has been redescribed by BROWN (1980). Only minor differences were found between his material and ours (Table 1). The ceratal core variations found in the Pacific animals did not exhibit the range observed in Britain. *Cuthona pustulata* is known from Brittany, France to Iceland (BROWN, 1980). The addition of a locality in the northeastern Pacific suggests that it is an

amphi-boreal species which can be expected to range further northward in the Pacific.

Cuthona pustulata can be distinguished from sympatric tergipidid species in the northeastern Pacific. *Cuthona albocrusta* has short, inflated cerata with pointed tips rather than elongate, cylindrical ones; *Catriona columbiana* has orange rhinophore bands and white ceratal lines; *Cuthona concinna* has purple or brown hepatic lobes in the cerata, and *C. divae* has a greater number of cerata which extend anterior to the rhinophores. None of these sympatric species have large, opaque white spots on the cerata. There are significant internal differences as well. *Cuthona concinna* and *C. divae* lack a penial stylet. *Cuthona albocrusta* has more radular teeth (56-70) as does *Catriona columbiana*, which has a strongly tapered radula with a pre-radular tooth and upwards of 100 teeth. None of these species is found living on hydroids belonging to the genus *Halecium*.

ACKNOWLEDGMENTS

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The Ecology of *Parvilucina tenuisculpta* (Carpenter, 1864) (Bivalvia: Lucinidae) on the Southern California Borderland

by

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Abstract. The pelecypod *Parvilucina tenuisculpta* (Carpenter, 1864) is a widely distributed member of the benthos of the southern California borderland where it is a prominent faunal element of every major habitat except the deep basins. In this fairly wide range of environments it lives with a large number of other taxa which may differ markedly from one location to another. The population densities of *Parvilucina* were highest in two very dissimilar environments—the insular shelf of the northern Channel Islands and the central part of the mainland shelf (Santa Monica Bay and San Pedro Bay). The insular shelf is primarily a non-depositional environment where relatively strong currents result in the development of coarse sediments rich in biogenic calcium carbonate components. The area is influenced by persistent upwelling. By contrast, the parts of the mainland shelf where population densities of *Parvilucina* were highest are in equilibrium environments highly influenced by the release of sewage wastewaters. Organic enrichment, in one case upwelling and the other sewage wastewaters, may be the factor responsible for the areas of high population densities.

INTRODUCTION

THE SEA FLOOR OF southern California and northern Baja California is much more complex than continental shelves in most other areas of the world. The region is complex and different enough to have been designated by a special term, "the continental borderland" (SHEPARD & EMERY, 1941; UCHUPI & EMERY, 1963). The part of the borderland that forms the Southern California Bight includes islands, banks, ridges, basins, and troughs. The bathymetry spans the range from the sublittoral zone to the bathyal depths (EMERY, 1960). Numerous submarine canyons transect the mainland and island shelves, descending toward and into the basins. Imposed upon this structural variety is a highly diverse substrate pattern. Consequently, the sea floor of the Bight consists of a very complex set of benthic habitats, and the diversity of the benthic macrofauna reflects this complex habitat (EMERY, 1960; FAUCHALD & JONES, 1978, 1979a, b; HARTMAN, 1955,

1956, 1963, 1966; HARTMAN & BARNARD, 1958, 1960; JONES, 1969).

The pelecypod *Parvilucina tenuisculpta* (Carpenter, 1864) (= *Lucina tenuisculpta*) (Figure 1) is an important member of the benthos of the southern California continental borderland. It has been collected in most of the major quantitative studies of the benthic macrofauna of the borderland. The purpose of this paper is to review these findings and to document the distribution, abundance, spatial and temporal variation, feeding and faunal associates of *P. tenuisculpta* in the region.

In an extensive survey of the benthos of the San Pedro Basin, HARTMAN (1955, 1966) recorded the biological components of 267 samples. WILSON (1956) reported *Parvilucina* in 18 of Hartman's samples. The population densities varied from 4 to 72 per m² (mean = 24.4/m²) in depths ranging from 14.6 to 702.5 m (mean = 178.7 m). In a paper on the dominant benthic molluscan faunas of the San Pedro Basin based on Wilson's data, BANDY (1958) included *Parvilucina tenuisculpta* as one of the elements of his Fauna 2 (dominant pelecypod faunas; the other members of this faunal group are *Nuculana taphria*, *Solamen columbianum*, *Solemya panamensis*, *Solen rosaceus* and *Thyasira barbarensis*). *Parvilucina* was reported only once (Sta-

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tion 3492, 3 specimens in 47.3 m) by HARTMAN (1956) in her study of the benthic macrofauna of Santa Monica Bay, but most of the molluscan specimens collected in this survey were not identified to species.

From 1956 to 1961, the California Water Quality Control Board supported an extensive investigation of the oceanography, geology, and marine biology of the mainland shelf of southern California. During the study the benthic macrofauna was sampled at 456 locations (AHF: USC, 1965). *Parvilucina tenuisculpta* was collected at 78 (17%) of the sampling locations of this study with population densities ranging from 4 to 68 per m² (mean = 12.0/m²) in water depths ranging from 13 to 253 m (mean = 66.5 m). It was absent from the 121 Van Veen grab samples collected from the shallower portion (2.4 to 10.1 m) of the shelf.

In her study of the benthic macrofauna of the submarine canyons of the borderland HARTMAN (1963) reported *Parvilucina* from Hueneme and Redondo submarine canyons. In their study of the benthos of the basins of the borderland HARTMAN & BARNARD (1958, 1960) did not record *Parvilucina* as a faunal element of any basin.

Working with a group of Allan Hancock Foundation scientists, FAUCHALD (1971) studied the impact of the Santa Barbara oil spill (1969) on the biota of the Santa Barbara shelf. *Parvilucina tenuisculpta* (reported as *Phacoides tenuisculpta*) was collected in more than 10% of the 85 samples in this study.

In a survey of the mainland shelf conducted by the Southern California Coastal Water Research Project (SCCWRP) in 1977, benthic samples were collected at intervals of approximately 10 km at a depth of 60 m along the entire length of the mainland shelf from Point Conception to the US-Mexican border. Very high densities of *Parvilucina*, approaching 10,000/m², were encountered off the Palos Verdes Peninsula and in Santa Monica Bay; densities along the 60-m transect north and south of these two areas were very much lower by comparison (WORD & MEARNS, 1978; fig. 4).

The present paper is based on data gathered during two major studies of the benthos of southern California funded by the Bureau of Land Management, the Baseline Study (1975–1976) and the Benchmark Study (1976–1977). These two studies, together, are the largest investigations of this kind ever made in this marine region (FAUCHALD & JONES, 1978, 1979a, b).

The benthic macrofauna was sampled at over 700 locations during the Baseline Study; 546 of these sampling locations were grouped in 11 regular grids termed High Density Sampling Areas (HDSAs); within these grids sampling stations were arranged on 1.7-km (1-mile) centers. These grids varied in size from 16 to over 100 sampling locations. Four of these HDSAs were on the mainland shelf and its slopes; one was on the Santa Catalina Ridge; two were on the insular shelf of the Channel Islands; and four were on the Santa Rosa-Cortes Ridge.

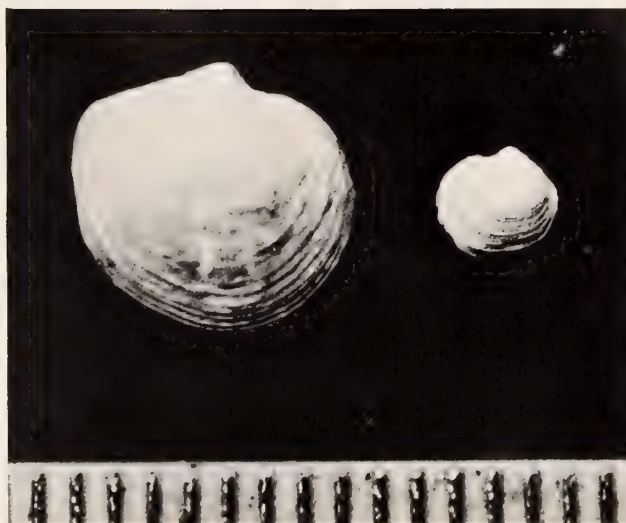


Figure 1

Parvilucina tenuisculpta (Carpenter, 1864). Larger specimens are from an outfall area; smaller specimens from near Point Conception. Scale in millimeters.

Another 227 sampling stations were located outside the HDSAs.

During the Benchmark Study, replicate sampling was conducted at 21 sampling stations in six areas of the borderland: off Coal Oil Point and the slope of the Santa Barbara Basin (3 stations); off San Pedro, on the slope of San Pedro Basin and within the basin (6 stations); south of San Miguel Island (2 stations); south of Santa Rosa Island (1 station); on the northern portion of the Santa Rosa-Cortes Ridge south of Santa Rosa Island, the slope of Santa Cruz Basin and within the basin (3 stations); and on the southern portion of the Santa Rosa-Cortes Ridge, including Tanner Bank, the slope of San Nicolas Basin and within the basin (6 stations). Sampling was conducted twice during the year, once in the period of low water temperature (early spring) and once in the period of high water temperature (early fall). Eight replicate samples were collected at each station during each sampling period.

METHODS

In both the Baseline and Benchmark studies, a navigational system was used that could guarantee an accuracy of ± 30.5 m.

Samples were collected by a modified 1/16 m² USNEL-Reineck spade (or box) corer (HESSLER & JUMARS, 1974). A subsample of each core was collected for sedimentary analysis. Benthic samples were screened through 1.0 mm and 0.5 mm stainless steel screens using the overflow-barrel method. The benthic macrofaunal invertebrates were narcotized for 20 min in 6% magnesium chloride in sea-



Figure 2

Chart of southern California borderland showing locations where *Parvilucina tenuisculpta* was collected. Circle-size reflects population density; see legend.

water prior to killing and fixation; specimens were killed and fixed in 10% buffered seawater formalin; after 36 h samples were transferred to 70% ethanol for preservation.

The *rapid identification procedure* was used to analyze the benthic samples (FAUCHALD & JONES, 1978). Some taxa were identified to the specific level, whereas others were identified only to the familial or generic level under the limitations of this method. All taxa were identified to species (where possible) for 165 of the 712 samples collected during the Baseline Study and for all of the 318 samples collected during the Benchmark study.

The diet and mineral particle-size range used by *Parvilucina tenuisculpta* in the major benthic habitats of the southern California borderland were analyzed (THOMPSON, 1982). The gut contents of 20 specimens from all habitats, offshore and mainland shelves, near and away from sewage outfalls, winter and summer, were examined microscopically (10–100 \times) and the material categorized

into five food groups: (1) detrital aggregates, (2) single mineral particles, (3) particulate organic material, (4) animal remains, and (5) Foraminifera. The proportion of each of the food groups in total sample volume was estimated visually to the nearest 10%. The sizes of mineral particles ingested were measured to the nearest 10 μ m using a light microscope (1000 \times). Because of the small sample size obtained from each specimen, the gut contents of five specimens from Stations 805 and 806 were pooled. A total of 150 particles from 15 random fields were measured.

The spatial dispersion of *P. tenuisculpta* at two different sampling scales was determined using an Index of Dispersion (MORISITA, 1959).

Determination of the organisms associated with *Parvilucina* was based on the faunal composition of representative sample-sets each consisting of 10 samples.

Sedimentary analyses were made by geologists at Cal-

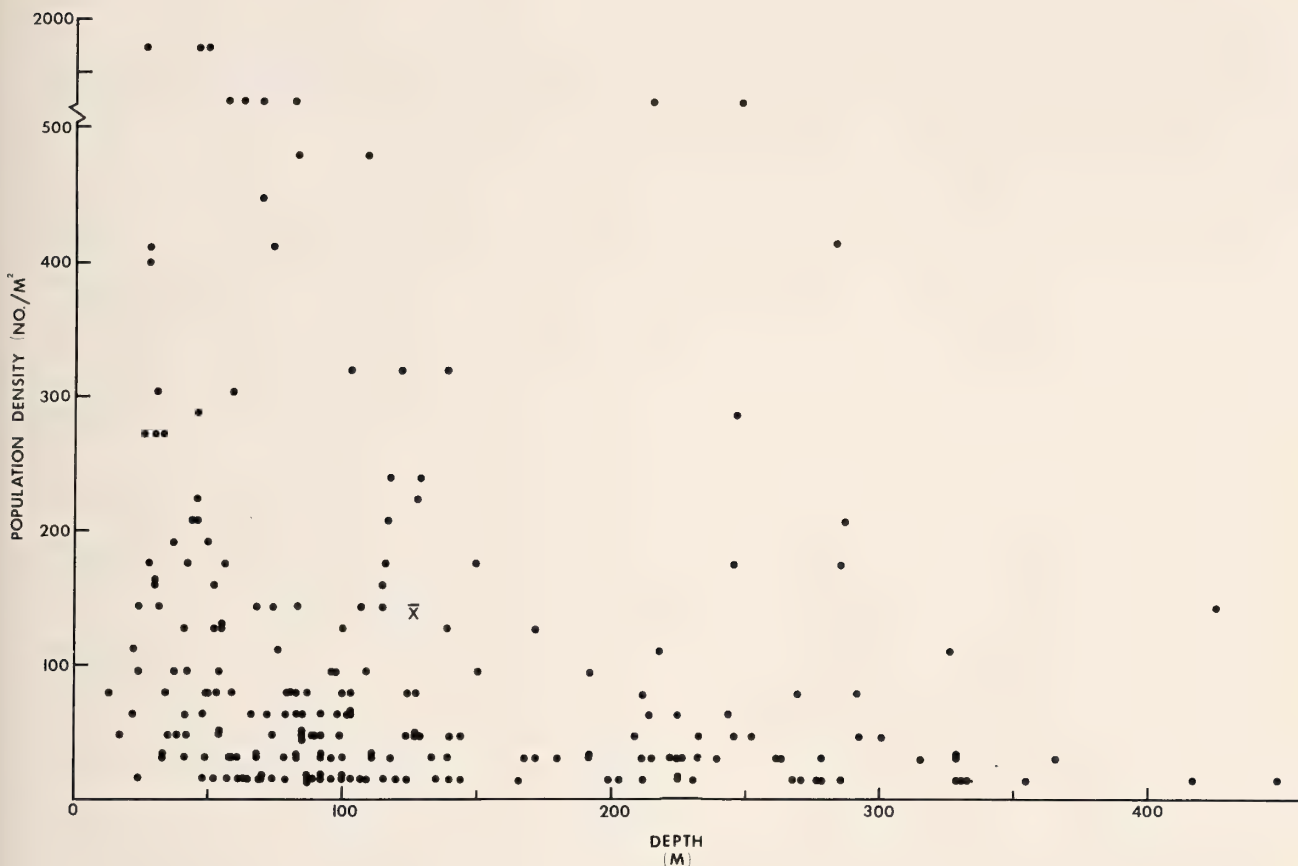


Figure 3

Depth distribution of *Parvilucina tenuisculpta* on the southern California borderland. The symbol \bar{x} indicates the position of the mean depth and the mean density.

ifornia State University, Northridge (Baseline Study) and University of California, Los Angeles (Benchmark Study).

RESULTS

Geographic Distribution

Parvilucina tenuisculpta is widely distributed throughout the southern California borderland (Figure 2). KEEN (1937) records the distribution of *Parvilucina tenuisculpta* as from 32°N to 60°N latitude (midpoint of range, 46°N) along the west North American coast, or approximately from Ensenada, Baja California to Cook Inlet, Alaska. It is a prominent faunal element of every major habitat type in the borderland except the deep basins. On the mainland shelf it occurs from Point Conception to the US-Mexican Border. It is an important element of the biota of the insular shelf of the Channel Islands and occurs on the Santa Rosa-Cortes Ridge including Tanner and Cortes Banks. It also occurs on the Santa Catalina Ridge north of Santa Catalina Island.

Parvilucina was collected at 226 (31.7%) of the 712 stations during the Baseline Study. Population densities ranged from 16 to 2560 individuals per m² (mean = 139.1/m²). Densities were highest in two very dissimilar environments—the insular shelf of the Channel Islands (the San Miguel Island HDSA and the Santa Rosa HDSA) and the central part of the mainland shelf in Santa Monica Bay and San Pedro Bay (including the Huntington Beach HDSA).

The insular shelf of the Channel Islands is primarily a nondepositional environment. Relatively strong currents result in winnowing of finer detrital sediments and the development of ripple marks. Sediments are frequently coarse and relatively high in calcium carbonate content, and the sediment patterns of the region tend to be complex. Evidence of bioturbation is minimal. The area may be influenced by the persistent upwelling centers of the Point Conception area (R. C. Dugdale, personal communication) and the upwelling resulting from the entrainment of deeper, subsurface water by the California Current across the Santa Rosa-Cortes Ridge (EMERY, 1960).

Table 1

A comparison of the habitat, depth and sediment characteristics of *Parvilucina tenuisculpta* on the Insular Shelves and the Mainland Shelf. Mean, range, and number of stations sampled are given for each variable.

Environmental variable	Insular shelf	Mainland shelf
Number/m ²	157.0 16–1872 (85 stations)	187.5 16–2560 (85 stations)
Depth (m)	124.0 26–416 (85 stations)	90.7 13–332 (85 stations)
Mean <i>phi</i>	3.3 1.4–4.4 (72 stations)	4.4 1.0–6.2 (67 stations)
Percent gravel	2.0 0.0–28.0 (72 stations)	1.0 0.0–57.0 (67 stations)
Percent sand	79.1 54.0–98.0 (72 stations)	49.8 3.0–99.0 (67 stations)
Percent silt	14.5 1.0–38.0 (72 stations)	42.1 0.0–84.0 (67 stations)
Percent clay	4.0 0.0–11.0 (72 stations)	7.1 2.0–23.0 (67 stations)
Percent CaCO ₃	21.7 3.1–54.8 (70 stations)	4.5 0.2–53.5 (53 stations)

Parvilucina was collected at 34 (72%) of the 47 stations comprising the San Miguel Island HDSA; population densities ranged from 16 to 544 individuals per m² (mean = 124.9/m²). It was present in 52 (51%) of the 102 stations forming the Santa Rosa Island HDSA; in this sampling grid, population densities ranged from 16 to 1872 individuals per m² (mean = 161.8/m²).

By contrast, the areas on the mainland shelf where densities of *Parvilucina* are high are equilibrium environments modified by man's activities, particularly the release of domestic and industrial wastewater into the marine environment. The combined discharge levels are in excess of one billion gallons of effluent per day (SCHAFFER, 1980). Except for areas of rock and relic sediments, sediments in this area are finer, much lower in calcium carbonate and higher in total organic content than on the insular shelf. Neither strong currents nor major upwelling are major factors in the area.

On the mainland shelf at 34 stations in Santa Monica Bay and San Pedro Bay, population densities ranged from 16 to 2560 individuals per m² (mean = 247.8/m²). Further south, in the Huntington Beach HDSA, *Parvilucina* occurred at 19 (73.1%) of the 26 stations comprising the grid, with population densities ranging from 32 to 380 individuals per m² (mean = 199.0/m²).

High population densities also were recorded on the mainland shelf in one other area, off Point Conception. At Station 830 the density was 1568 per m² and at Station 835 the density was 2192 per m².

Distribution by Depth

The depth distribution of *Parvilucina tenuisculpta* reflects the fact that this species primarily inhabits the topographic highs—shelves, ridges, and banks—of the borderland. The 226 sampling locations where it was collected ranged in depth from 13 to 433 m (mean = 126.6 m); the sampling locations on the insular shelf of the Channel Islands were somewhat deeper (range, 26–416 m; mean = 124.0 m) than those on the mainland shelf range, 13–322 m; mean = 90.7).

The depth distribution of this species on the southern California borderland is illustrated in Figure 3. Over half (54.4%) of the stations where *Parvilucina* was collected were in depths of 100 m or less, where the mean density was 177.7/m². Over 90% of all the samples containing *Parvilucina* were collected at depths of 300 m or less.

The 18 samples collected by HARTMAN (1955, 1966) and analyzed by WILSON (1956) had a considerably greater depth range than the samples collected during the BLM Projects; their San Pedro Bay samples were collected in depths ranging from 14.6 to 702.5 m (mean = 178.8). By contrast, the 78 samples collected from the mainland shelf during the Water Quality Control Project (AHF:USC, 1956) had a more limited range (13 to 253 m; mean = 66.5 m). Combining the data from these two surveys with that of the BLM study the overall range of this species in the borderland is from 13 to 702 m (mean = 114.7).

Distribution in Relation to Sediments

Data are available on the sedimentary characteristics of the substrate at most of the sampling locations (186 and 226) where *Parvilucina tenuisculpta* was collected. A comparison of the habitat of *Parvilucina* on the Channel Island shelf and the mainland shelf is presented in Table 1. Sediments, in general, are coarser on the insular shelf than on the mainland shelf (average mean *phi* of 3.3 compared to 4.4). An important difference between these two environments is that the calcium carbonate content of the sediments is much higher on the island shelf than on the mainland shelf (mean of 21.7% compared to 4.5%). This illustrates the fact that in the non-depositional environment of the insular shelves, biogenic contributions of calcium carbonate materials are a much more important sedimentological component than in the equilibrium environment of the mainland shelf.

Spatial and Temporal Variation

Limited information was available on the temporal variation of *Parvilucina tenuisculpta* populations. Only a single-year sequence (winter–summer) was analyzed and

Table 2

Average densities and indices of dispersion (I_b) and seasonal comparisons for *Parvilucina tenuisculpta* from benchmark sites. Samples were subdivided during sample processing into two sample fractions: the 1.0-mm fraction, all specimens collected on a 1.0-mm mesh screen and the 0.5-mm fraction, all specimens collected on a 0.5-mm screen. Density data are presented for each fraction.

Sta- tion	Depth (m)	Sample frac- tion (mm)	Winter				Summer				Mann- Whitney U _s winter <i>vs</i> summer
			Mean density (No./m ²)	I _b	χ ²	N	Mean density (No./m ²)	I _b	χ ²	N	
Mainland shelf											
819	32	1.0	10.1	3.20	15.8	8	2.0	0	7.0	8	50
		0.5	8.0			2	136.0			2	
801	68	1.0	22.1	2.33	20.3*	8	12.0	1.60	10.0	8	29
		0.5	32.0			2	48.8			2	
802	336	1.0	2.0	0	7.0	8	4.0	0	6.0	8	50
		0.5	0			2	0			2	
San Miguel Is. shelf											
806	99	1.0	148.0	1.38	35.0*	8	142.1	1.06	10.9	8	26
		0.5	56.0			2	64.0			2	
805	239	1.0	162.1	1.11	15.7	8	120.0	1.13	14.9	8	21.5
		0.5	48.0			2	48.0			2	
Santa Rosa Ridge											
808	105	1.0	9.6	1.67	5.3	5	0			8	12
		0.5	8			2	0			2	
809	225	1.0	49.9	1.95	29.7*	8	44.0	1.21	11.5	8	31.5
		0.5	8.0			2	0			2	
Tanner Bank											
815	100	1.0	12.0	2.13	12.7	8	12.0	3.20	18.0*	8	30
		0.5	0			2	0			2	
818	188	1.0	0	—	—	1	2.0	0	7.0	8	—
		0.5	0			1	8.0			2	
817	519	1.0	2.0	0	7.0	8	0	—	—	8	31.5
		0.5	0			2	0			2	

* = Significant value ($\chi^2 \geq 19.0$), $\alpha = 0.05$.

is interpreted cautiously. Seasonal differences in population density were not significantly different (Mann-Whitney U_s , $\alpha = 0.05$) at any of the sites sampled, even though at Stations 808, 817, and 818, specimens were collected at one season but not the other (Table 2).

At the mainland shelf sites (Stations 801, 819), most often the densities in the 0.5-mm fraction were greater than in the 1.0-mm fraction; in the Station 819 summer sample nearly 99% of the specimens were in the 0.5-mm fraction. These small specimens, mostly juveniles, may be evidence of recruitment, but none of the other summer samples contained such densities of juveniles.

To understand the spatial variation of *P. tenuisculpta*, three separate sample sets, each collected at a different spatial scale, were analyzed. Populations collected during the Benchmark Study (scale = 1 km) (Table 2) generally showed a tendency towards randomness; 13 samples were randomly dispersed and only 4 were aggregated among

the replicates. There were no apparent effects of density or presence of juveniles on aggregation.

Using SCCWRP data (Table 3), 10 samples were selected to represent each of three zones along sewage outfall gradients: "control," "transition," and "contaminated." Samples collected on a large scale (>1 km) indicated that the populations of *P. tenuisculpta* from all zones were highly aggregated. However, when sets of 10 replicates (scale \approx 20 m) were analyzed, the populations were randomly dispersed except in the "transition" zone where they exhibited aggregated dispersions and were most dense.

To summarize the results from these three sample sets, it appears that patches of *P. tenuisculpta* may exist at several scales. In "control" or "normal" areas, patches were detected at the kilometer scale, but near sewage outfalls, in the "transition" zone, patches apparently were more densely packed. The cause of this change in population structure in the "transition" zone is not clear.

Table 3

Average densities and indices of dispersion for two different sets of data on *Parvilucina tenuisculpta* from mainland shelf areas. N = 10.

Station	Mean density (No./m ²)	I _s	χ ²
Between zones, km scale			
Normal	84	3.49	215.3*
Transition	1304	1.64	877.0*
Contaminated	243	2.60	400.4*
Within zones, m scale			
Normal			
3-3	15	1.05	9.7
4-3	56	0.99	8.6
22-2	25	0.90	6.6
24-2	59	0.95	13.4
Transition			
5-4	3568	1.03	115.6*
59	1844	1.03	56.5*
8-3	424	1.16	74.3*
Contaminated			
7-3	25	1.23	14.6

* = Significant value ($\chi^2 \geq 19$; $\alpha = 0.05$).

Diet

Parvilucina has been collected to a depth of 6 cm below the surface (BALCOM, 1980) indicating that it may feed at or below the sediment surface. This species has a short

incurrent siphon and a muscular pharynx. In some of the specimens examined, the mantle cavity and ctenidia contained many large (>50 μm) single mineral particles. In three specimens examined from the offshore insular shelf (Stations 805, 806), the pharynx contained 2–5 of these particles (59–216 μm). The digestive tracts contained mostly detrital aggregates (aggregations of clay mineral particles, organic material, and microbes). By volume, mineral particles up to 100 μm occurred in the gut contents (Figure 4). No spatial or temporal variation in gut contents was observed in the 20 specimens examined.

It is believed that *P. tenuisculpta* ingests primarily organic rich detrital aggregates from fine sediment on the mainland shelf, but in areas where coarser sediments predominate (offshore shelves, ridges and banks) it may ingest larger single mineral particles, either to remove organic encrustations and microbes or to use as "mill stones" in the pharynx to crush other food items.

Preliminary analysis of the tissues of *Parvilucina* has revealed the presence of endosymbiotic bacteria that can oxidize sulfide to obtain metabolic energy (FELBECK *et al.*, 1981). Populations of *P. tenuisculpta* living near outfalls may utilize this alternative energy source in addition to normal food resources, which could explain the reported increase in size of the clams living near the outfalls (WORD *et al.*, 1977).

Macrofaunal Associates

Determination of the organisms associated with *Parvilucina tenuisculpta* has been made for the two dissimilar

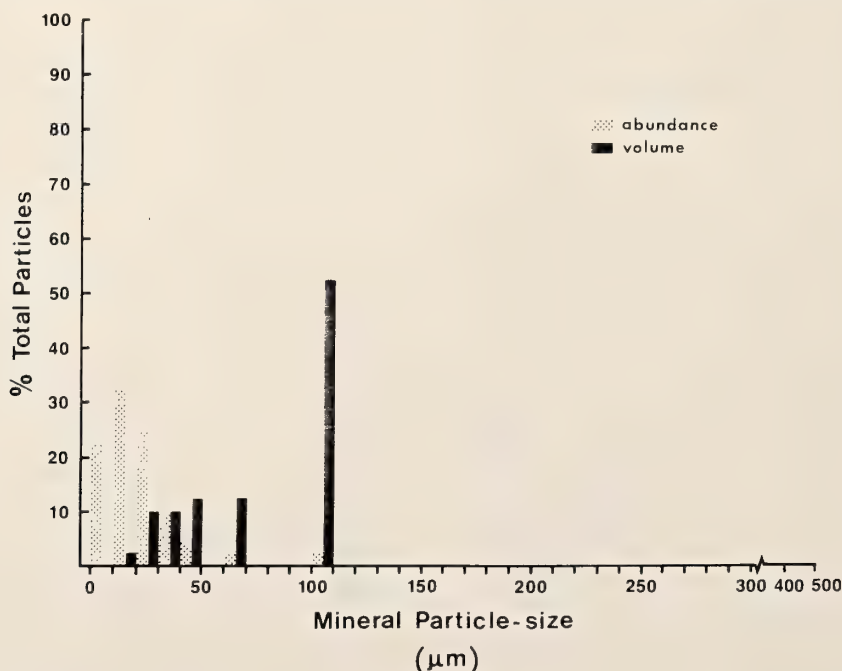


Figure 4

Average mineral particle-size distribution from guts of *Parvilucina tenuisculpta* collected from the insular shelves.

Table 4a

The numerically dominant faunal associates of *Parvilucina tenuisculpta* in 10 representative samples from the Huntington-Laguna High Density Sampling Area. Abbreviations: crust. = crustacean; gastro. = gastropod; pelec. = pelecypod; poly. = polychaete; and oph. = ophiuroid.

Rank	Name of species	Major taxon	Density (No./m ²) (mean \pm SD)	Frequency
1	<i>Euphilomedes producta</i>	crust.	1212 (\pm 2076.1)	0.5
2	<i>Euphilomedes carcharodonta</i>	crust.	630 (\pm 698.9)	0.9
3	<i>Parvilucina tenuisculpta</i>	pelec.	279 (\pm 126.9)	1.0
4	<i>Lumbrineris</i> spp. (6 species)	poly.	134 (\pm 144.0)	0.9
5	<i>Mediomastus californiensis</i>	poly.	130 (\pm 115.9)	1.0
6	<i>Amphiodia urtica</i>	oph.	122 (\pm 90.8)	1.0
7	<i>Prionospio</i> cf. <i>malmgreni</i>	poly.	114 (\pm 99.0)	0.9
8	<i>Axinopsida serricata</i>	pelec.	94 (\pm 61.7)	1.0
9	<i>Glyceria</i> spp. (4 species)	poly.	91 (\pm 44.7)	0.9
10	<i>Heterophoxus oculatus</i>	crust.	75 (\pm 81.6)	0.7
11	<i>Pectinaria californiensis</i>	poly.	72 (\pm 114.8)	0.7
12	<i>Macoma yoldiformis</i> ; <i>Macoma</i> sp.	pelec.	62 (\pm 52.8)	0.9
13	<i>Mysella tumida</i>	pelec.	48 (\pm 44.9)	0.9
14	<i>Compsomyx subdiaphana</i>	pelec.	30 (\pm 37.5)	0.6
15	<i>Tellina carpenteri</i>	pelec.	18 (\pm 19.5)	0.6
15	<i>Westwoodilla caecula</i>	crust.	18 (\pm 19.5)	0.6
15	<i>Rictaxis punctocoelata</i>	gastro.	18 (\pm 20.8)	0.5

Table 4b

The numerically dominant faunal associates of *Parvilucina tenuisculpta* in 10 representative samples from the mainland shelf of Santa Monica Bay and San Pedro Bay. Abbreviations as in Table 4a.

Rank	Name of species	Major taxon	Density (No./m ²) (mean \pm SD)	Frequency
1	<i>Parvilucina tenuisculpta</i>	pelec.	789 (\pm 734.1)	1.0
2	<i>Axinopsida serricata</i>	pelec.	378 (\pm 460.4)	0.9
3	<i>Euphilomedes carcharodonta</i>	crust.	158 (\pm 174.3)	0.7
4	<i>Lumbrineris</i> spp. (2 species)	poly.	93 (\pm 92.8)	0.9
5	<i>Pectinaria californiensis</i>	poly.	78 (\pm 88.4)	0.7
6	<i>Heterophoxus oculatus</i>	crust.	69 (\pm 89.5)	0.5
7	<i>Glyceria</i> sp.	poly.	50 (\pm 49.6)	0.9
8	<i>Prionospio</i> cf. <i>malmgreni</i>	poly.	46 (\pm 47.7)	0.6
9	<i>Tellina carpenteri</i>	pelec.	22 (\pm 23.9)	0.7
9	<i>Mysella tumida</i>	pelec.	22 (\pm 43.7)	0.5
11	<i>Goniada</i> sp.	poly.	19 (\pm 22.4)	0.5

borderland environments where it is most frequent and abundant, the mainland shelf and the Channel Islands shelf. The faunal composition of four representative sample sets, one from each of the areas, has been examined: on the mainland shelf, the Huntington Beach HDSA (Table 4a) and the Santa Monica Bay and San Pedro Bay shelves (Table 4b) and on the insular shelf, the San Miguel HDSA (Table 4c) and the Santa Rosa HDSA (Table 4d). The 10 samples selected to represent each area were those in which *Parvilucina* was most abundant.

The numerically dominant taxa varied considerably and only a few were dominant in all four areas; these included

the polychaetes *Prionospio* cf. *malmgreni*, *Lumbrineris* spp. and *Glyceria* spp., and the mollusk *Tellina carpenteri*. Several other species were numerically dominant in three of the four areas, including the polychaete *Pectinaria californiensis*, the crustaceans *Euphilomedes carcharodonta* and *Heterophoxus oculatus*, and the echinoderm *Amphiodia urtica*.

Species richness was somewhat greater at the insular shelf locations (Santa Rosa Island sample set, 250 taxa; San Miguel Island sample set, 198 taxa) than at the mainland shelf locations (Santa Monica Bay-San Pedro Bay sample set, 184 taxa; Huntington Beach sample set, 166

Table 4c

The numerically dominant faunal associates of *Parvilucina tenuisculpta* in 10 representative samples from the San Miguel Island High Density Sampling Area. Abbreviations as in Table 4a.

Rank	Name of species	Major taxon	Density (No./m ²) (mean \pm SD)	Frequency
1	<i>Parvilucina tenuisculpta</i>	pelec.	256 (\pm 109.7)	1.0
2	<i>Amphiodia urtica</i>	oph.	237 (\pm 158.0)	1.0
3	<i>Paraphoxus bicuspidatus</i>	crust.	51 (\pm 32.6)	0.9
4	<i>Lumbrineris</i> spp. (7 species)	poly.	50 (\pm 56.1)	0.7
5	<i>Prionospio</i> cf. <i>malmgreni</i>	poly.	48 (\pm 29.5)	0.9
6	<i>Onuphis</i> spp. (2 species)	poly.	40 (\pm 66.1)	0.6
7	<i>Ampelisca pacifica</i>	crust.	37 (\pm 22.9)	1.0
8	<i>Heterophoxus oculatus</i>	crust.	35 (\pm 31.8)	0.7
9	<i>Pista</i> sp. B; <i>Pista</i> sp.	poly.	34 (\pm 25.2)	0.9
10	<i>Mediomastus californiensis</i>	poly.	32 (\pm 37.2)	0.5
11	<i>Tellina carpenteri</i>	pelec.	30 (\pm 36.8)	0.7
11	<i>Tomburchus redondoensis</i>	pelec.	30 (\pm 28.1)	0.6
13	<i>Amphissa undata</i>	gastro.	29 (\pm 29.0)	0.7
13	<i>Dougalopus amphicantha</i>	oph.	29 (\pm 27.5)	0.6
13	<i>Glycera</i> spp. (2 species)	poly.	29 (\pm 36.5)	0.6
16	<i>Aricidea</i> cf. <i>longicirrata</i> ; <i>Aricidea</i> sp.	poly.	24 (\pm 27.0)	0.8
16	<i>Nephtys ferruginea</i>	poly.	24 (\pm 22.9)	0.6
18	<i>Notomastus</i> spp. (2 species)	poly.	22 (\pm 23.9)	0.7
18	<i>Aoroides columbiae</i>	crust.	22 (\pm 29.7)	0.5
20	<i>Polycirrus</i> sp.	poly.	21 (\pm 25.8)	0.5
21	<i>Leptochelia</i> sp.	crust.	19 (\pm 21.2)	0.5
22	<i>Pholoe glabra</i>	poly.	18 (\pm 13.3)	0.7
22	<i>Byblis veleronis</i>	crust.	18 (\pm 20.8)	0.5
24	<i>Pectinaria californiensis</i>	poly.	16 (\pm 14.3)	0.6

Table 4d

The numerically dominant faunal associates of *Parvilucina tenuisculpta* in 10 representative samples from the Santa Rosa Island High Density Sampling Area. Abbreviations as in Table 4a.

Rank	Name of species	Major taxon	Density (No./m ²) (mean \pm SD)	Frequency
1	<i>Parvilucina tenuisculpta</i>	pelec.	602 (\pm 488.9)	1.0
2	<i>Lumbrineris</i> spp. (4 species)	poly.	101 (\pm 81.6)	1.0
3	<i>Euphilomedes carcharodonta</i>	crust.	91 (\pm 211.7)	0.5
4	<i>Tellina carpenteri</i>	pelec.	78 (\pm 78.2)	0.9
5	<i>Nephtys</i> spp. (3 species)	poly.	54 (\pm 69.5)	0.7
6	<i>Pholoe glabra</i>	poly.	51 (\pm 60.6)	0.6
7	<i>Glycera oxycephalis</i> ; <i>Glycera</i> sp.	poly.	45 (\pm 63.5)	0.7
7	<i>Ampelisca pugetica</i>	crust.	45 (\pm 75.3)	0.6
9	<i>Amphiodia urtica</i>	oph.	38 (\pm 35.2)	0.6
10	<i>Aricidea wassi</i> ; <i>Aricidea</i> sp.	poly.	35 (\pm 34.9)	0.7
11	<i>Driloneris falcata</i>	poly.	26 (\pm 32.2)	0.5
11	<i>Prionospio</i> cf. <i>malmgreni</i>	poly.	26 (\pm 35.2)	0.5
13	<i>Pista</i> sp. B; <i>Pista</i> sp.	poly.	22 (\pm 24.9)	0.6
14	<i>Byblis veleronis</i>	crust.	21 (\pm 21.5)	0.5
15	<i>Artacamella hancocki</i>	poly.	18 (\pm 16.6)	0.6

taxa). In all four areas, over half of the taxa were recorded only once in the respective sample sets, indicating a relatively high level of diversity in all of these areas.

SUMMARY AND DISCUSSION

The pelecypod *Parvilucina tenuisculpta* is an important, widely distributed member of the benthos of the southern

California borderland, where it is a prominent faunal element of every major habitat type except the deep basins. The population densities of this species were highest in two very dissimilar environments—the insular shelf of the northern Channel Islands and the central part of the mainland shelf (Santa Monica Bay and San Pedro Bay). The insular shelf is primarily a non-depositional environment. Relatively strong currents result in the winnowing of finer detrital sediments, and the development of coarse sediments rich in biogenic calcium carbonate components. The area is influenced by persistent upwelling. By contrast, the parts of the mainland shelf where densities are highest are in environments highly influenced by man's activities, particularly the release of sewage wastewaters into the marine environment.

Parvilucina appears to exhibit little temporal variation, but the data are inadequate to make firm conclusions. Populations of *Parvilucina* are patchy on a large scale (km), but within patches they are usually randomly dispersed, except in the areas near sewage outfalls, where the scale of heterogeneity is approximately 20 m and densities are the highest measured in the region. The reasons for this change in population structure are not clear.

A diverse array of macrofaunal taxa is associated with *Parvilucina*. The numerically dominant taxa varied considerably from location to location, and only a few were dominant in the four representative sample sets examined in this study.

Parvilucina has been identified as a co-dominant element in a faunal assemblage on the Santa Rosa-Cortes Ridge. Combining the results derived from classification and recurrent group analysis, FAUCHALD & JONES (1979b) identified 13 species groups from the continental borderland. Four of these groups were on the Santa Rosa-Cortes Ridge and Tanner Bank (Stations 805, 806, 809, 815, 816, and 818). Three of the groups were ophiuroid-dominated assemblages: the *Amphiodia urtica* assemblage; the *Amphipholis squamata*-*Golfingia minuta* assemblage and the *Amphiura acrystata*-*Ampelisca cristata* assemblage. The fourth assemblage, the *Lumbrineris cruzensis*-*Parvilucina tenuisculpta* assemblage, is a loosely aggregated species group that occurred at most of the offshore stations. The principal faunal components of this assemblage are: the polychaetes *Chloeia pinnata*, *Decamastus gracilis*, *Acesta ceterinae*, *Acestra* cf. *assimilis*, *Glycera tessellata*, *Travisia brevis*, and *Euchone hancocki*; the mollusks *Amphissa undata* and *Tomburchus redondensis*; the crustaceans *Byblis veleronis*, *Ampelisca pugetica*, *Diastylis* sp. A., *Maera simile*, and *Photis lacia*; and the echinoderm *Amphiodia urtica*. Only half of these species occurred in the two mainland shelf sample-sets, all at a frequency of 4 or less out of 10 samples, whereas 75% of them were present in the two insular shelf sample sets at frequencies up to 7 samples out of 10 (Tables 4a-d).

Ecologically *Parvilucina* appears to be able to live in a fairly wide range of environments populated by a large

number of other taxa which may differ markedly from one location to another.

The two most interesting questions concerning the ecology of *Parvilucina* on the borderland are: (1) why have the frequency and abundance of this species on the mainland shelf increased so dramatically (from a mean of 12.0/m² to 186.5/m²) in approximately 20 years? and (2) what factor or factors lead to a high density of this species in two areas that are quite dissimilar in most respects?

The load of wastewaters contributed to the marine environment has increased markedly over the last 20 years, and this change could easily explain the elevated population densities of *Parvilucina* on the affected parts of the mainland shelf.

The insular shelf, an area of clean water, also is an area of high organic enrichment, although the source of this enrichment, upwelling, is very different from that on the central portion of the mainland shelf. In another upwelling area, at Point Conception on the mainland shelf, population densities also are high.

Parvilucina ingests fine detrital aggregates. It may feed at the sediment surface, or below the surface, and may process large mineral particles to obtain food. This species also may use endosymbiotic bacteria to oxidize sulfide near outfalls, thereby deriving additional energy, which may allow it to grow larger than in other areas.

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Hybridization of Two Populations of a Marine Opisthobranch with Different Developmental Patterns

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Abstract. Two populations of the ascoglossan opisthobranch *Elysia chlorotica* (Gould, 1870) have different reproductive modes. In one population, from Martha's Vineyard, Massachusetts, veliger larvae hatched from egg masses and fed on phytoplankton prior to metamorphosis. In the second population, from Ipswich, Massachusetts, the majority of veligers completed development up to and including metamorphosis in egg capsules before hatching. The Ipswich population laid egg masses with fewer eggs, and both eggs and egg capsules were larger than those of the Martha's Vineyard population.

Both populations can be cultured in the laboratory. The Ipswich population was cultured both in dilute (17‰) and full strength (33‰) seawater. In laboratory culture, Ipswich larvae metamorphosed in the egg capsule without substrate, but metamorphosis of the planktonic veligers (Martha's Vineyard) required the alga *Vaucheria* sp.

Laboratory-reared individuals from the two populations hybridized. F₁ egg masses had either large Ipswich-type egg capsules or smaller Martha's Vineyard-type egg capsules. The majority of veligers from F₁ Ipswich-type capsules remained in capsules up to metamorphosis. All veligers from F₁ Martha's Vineyard-type capsules hatched prior to metamorphosis. In F₂ egg masses, capsule size was intermediate between the Ipswich and Martha's Vineyard size classes. All F₂ veligers hatched prior to metamorphosis and required *Vaucheria* sp. for metamorphosis.

INTRODUCTION

THOMPSON (1967, 1976) divided opisthobranch development into three distinct categories—planktotrophic, lecithotrophic, and direct development. Development in each category differs with respect to the size and number of eggs produced and the stage of development reached when veligers hatch from egg masses. In general, planktonic developers produce many small eggs which hatch prior to metamorphosis. Lecithotrophic developers produce fewer intermediate-sized eggs which hatch prior to metamor-

phosis but after a longer embryonic period than planktonic developers. Direct developers produce a much smaller number of large eggs and remain encapsulated up to metamorphosis.

BONAR (1978) has refined THOMPSON's scheme and defined two variations within the category of direct development. In some cases of direct development—referred to as ametamorphic capsular development—embryos do not develop into a distinct veliger stage and, therefore, do not undergo metamorphosis before hatching as juveniles. In other cases—referred to as capsular metamorphic development—embryos develop into a distinct veliger stage but do not hatch out of capsules prior to metamorphosis.

Most species of opisthobranch are limited to one of the

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reproductive patterns outlined by THOMPSON and refined by BONAR. However, there are reports of more than one reproductive pattern within a species (FRANZ, 1971; RIVEST, 1978; EYSTER, 1979; CLARK *et al.*, 1979). In only one case (EYSTER, 1979) was an attempt made to determine whether distinct differences in developmental pattern between members of a species were accompanied by reproductive isolation.

This report compares the different reproductive patterns in two populations of the euryhaline ascoglossan opisthobranch *Elysia chlorotica* (Gould, 1870). Planktotrophic development already has been described for the species (HARRIGAN & ALKON, 1978a). We describe here the capsular metamorphic type of direct development in a second population.

If this is a true case of developmental variability within a species (poecilogony), crosses between individuals from the different populations should produce viable hybrid offspring. It was the purpose of this study to determine whether the two populations could be cultured and hybridized and to compare the reproductive traits expressed in the field-collected, laboratory-reared, and hybrid generations.

MATERIALS AND METHODS

Culture of Algae

Successful culture of *Elysia chlorotica* depends upon the culture of appropriate algal food sources for both adult and larval stages. Adults feed on various species of the alga *Vaucheria*; the veligers require unicellular algae. Mats of substrate, containing filaments of *Vaucheria compacta* (Collins) Collins, were collected in salt marshes and placed in petri dishes moistened with seawater. The mats were kept in an incubator at 15°C on an 18-h light:6-h dark cycle. Light was supplied by six fluorescent bulbs. A second species, *Vaucheria litorea* C. Agardh, also collected from salt marshes, was grown submerged in "f/2" algal medium of GUILLARD (1975) under the same conditions. The unicellular alga *Chroomonas* (strain 3C), used to feed the veligers, was cultured in "f/2" medium under the same conditions as *Vaucheria*.

Culture of Encapsulated Larvae

Approximately 100 adult animals collected from Ipswich, Massachusetts were placed in glass baking dishes containing seawater of salinity 33 parts per thousand (‰) which was changed every other day. The animals were kept in an incubator at 18–19°C on a 12-h light:12-h dark cycle. Light was provided by four fluorescent bulbs. *Vaucheria compacta*, often attached to marsh sediment, was placed with the animals as a food source. Egg masses were collected daily and each egg mass was transferred to a small, glass petri dish containing seawater filtered through a Millipore membrane (0.45 µm pore). In order to classify

the development type, the following observations and measurements were made: (1) the number of eggs per egg mass was determined in six egg masses by counting the number of eggs in 5 mm of egg mass, dividing by 5, and multiplying the result by the total length of egg mass; (2) the size of five uncleaved eggs and their capsules was measured using an ocular micrometer and compound light microscope; and (3) the number of days to veliger stage, eyespot formation, and metamorphosis was recorded. In addition, adult sizes were recorded as unrelaxed length using a millimeter rule.

Elysia chlorotica inhabits low salinity marshes. In the course of collecting slugs we measured salinities from 3 to 32‰. Because this is such a wide range of salinities, the effect of salinity on development was investigated. Adults from Ipswich, Massachusetts were kept in dilute seawater (17‰). Egg masses were collected from these adults and the pattern of development was observed to determine the effect salinity had on development.

Culture of Planktonic Veligers

Ten adults collected from Menemsha Pond, Martha's Vineyard, Massachusetts in the fall of 1979 survived over winter and laid egg masses in the spring of 1980. Egg masses were isolated and veligers maintained up to metamorphosis according to the general methods described by HARRIGAN & ALKON (1978a). Measurements of (1) the number of eggs per egg mass, (2) the size of eggs and egg capsules, and (3) the size of adults, were made as previously described. The time required for veligers to reach various stages of development was determined. Veligers were ready to hatch shortly after the development of a black pigment band on the dorsal surface behind the velum. At this stage, the egg masses were teased open, and the veligers released were washed in seawater filtered through Millipore membranes (0.22 µm pore) with Rifampicin added (5 mg/L). Approximately 1000 veligers were transferred to each of three 1-liter beakers containing 800 mL of filtered (0.22 µm) seawater containing Rifampicin (5 mg/L). Cetyl alcohol was sprinkled on the surface of the culture to prevent the veligers from being caught in the surface tension (HURST, 1967). Beakers were covered with plastic to minimize contamination by dust. Seawater in the beakers was changed three times a week. To separate veligers from culture water, cultures were gently poured through 44-µm plankton netting stretched across the diameter of a piece of plastic (PVC) pipe. The pipe was held upright in a finger bowl filled with seawater such that the plankton net and veligers were always below the surface of the water. Veligers concentrated above the plankton netting were washed with fresh seawater then transferred with a pipette to beakers of fresh seawater and Rifampicin.

The veligers were fed *Chroomonas* six days a week. After determining the cell count of algal cultures with a hemocytometer, a sufficient volume of algal cells was added

to the veliger cultures to yield a final cell count of 3 to 5 cells/ μ L.

The veligers were judged competent to metamorphose on the basis of three criteria: (1) development of eyespots; (2) development of a propodium; and (3) enlargement of the black pigment patch initially located immediately posterior to the velum over the entire dorsal surface of the larva. Once judged competent, groups of 50 veligers were placed in culture dishes containing 100 mL of coarse-filtered (1 μ m) seawater and filaments of *Vaucheria*. Veligers attached to the algae and metamorphosed. Subsequently juveniles were transferred to larger culture dishes and eventually into aquaria. The juveniles were continuously fed *Vaucheria compacta* because it was the most abundant *Vaucheria* species. The number of veligers surviving up to metamorphosis and the number that subsequently metamorphosed were determined.

Metamorphosis on Different Algal Substrates

A separate experiment was performed to determine whether other substrates could be used for metamorphosis. One hundred veligers were placed in culture dishes with either *Vaucheria compacta*, *V. litorea*, *Enteromorpha* sp., or *Bryopsis plumosa* (Hudson) C. Agardh (all collected from Martha's Vineyard), and the number of metamorphosed juveniles was counted. *Enteromorpha* sp. was chosen because it represents a major part of the pond flora. *Bryopsis* is not common in the pond but one species of this genus has previously been identified as a food source for other ascoglossan species (GREENE, 1970).

Laboratory Crosses—Parental, F₁, and F₂ Generations

Parents for the crosses were the offspring from egg masses laid by field-collected Ipswich and Martha's Vineyard adults. These offspring were raised according to the culture procedures described above except that all animals were raised at room temperature (25°C). Measurements of the characteristics of parental egg masses were made on the egg masses collected from crosses of the field-collected adults—Ipswich \times Ipswich and Martha's Vineyard \times Martha's Vineyard. Length of egg capsules, length of veliger shells, and the days to hatching after egg-mass deposition were recorded in 10 egg masses of each type. Directly following metamorphosis, 10 offspring from each developmental type were isolated. Each Ipswich offspring was placed with a Martha's Vineyard offspring to form a mating pair (Ipswich \times Martha's Vineyard). Because the species is hermaphroditic, each individual in a cross could serve as both male and female. Egg masses from these parental mating pairs were the F₁ egg masses that gave rise to the F₁ adult generation.

Each F₁ egg mass was scored according to parental affinity. A Martha's Vineyard-type F₁ egg mass was defined as having all egg capsules of small length and veligers that hatched with no eyespots or propodium. An Ips-

wich-type egg mass had large capsules and veligers that either hatched with eyespots and propodium late in development or metamorphosed in capsules. Measurements of capsule length, veliger shell length, and days to hatching were made from 10 F₁ Martha's Vineyard-type egg masses and 10 F₁ Ipswich-type egg masses. Offspring from F₁ Martha's Vineyard-type egg masses and F₁ Ipswich-type egg masses were isolated directly following metamorphosis. Ten mating pairs were formed by placing one offspring from a Martha's Vineyard-type egg mass with one offspring from an Ipswich-type egg mass (Ipswich F₁ \times Martha's Vineyard F₁). Egg masses from these F₁ crosses were the F₂ egg masses that gave rise to the F₂ generation. Measurements of capsule length, veliger shell length, and days to hatching were made on 10 of these F₂ egg masses.

To determine whether the slugs self-fertilized, newly metamorphosed offspring from parental egg masses of each developmental type were isolated and observed for possible egg mass deposition. In addition, some newly metamorphosed individuals from parental egg masses of each developmental type were grouped together (Ipswich \times Ipswich and Martha's Vineyard \times Martha's Vineyard). The F₁ and F₂ generations produced by these intrapopulation crosses served as controls to monitor the effects of laboratory culture on developmental type.

RESULTS

Culture of Encapsulated Larvae

Developmental characteristics of the population from Ipswich, Massachusetts are listed in Table 1. Field collected animals had a mean length of 7.60 mm. The mean number of eggs/egg mass was 175.67. A distinctive feature of this development type was the relatively large diameter of the egg capsule in relation to egg diameter. The mean capsule length of 309.00 μ m was three times the mean diameter of the egg (96.00 μ m). In addition, the capsules and embryos were surrounded by a thick gelatinous layer. There was a statistically significant decrease in development time for egg masses raised in dilute seawater (Table 2). At both salinities the embryos reached the veliger stage in approximately three days. All veligers eventually developed black pigment bands on the dorsal surface of the velum. Eyespots appeared in larvae approximately six days after egg mass deposition in dilute seawater and nine days after deposition in full strength seawater. About two weeks were required for eggs in full strength seawater to develop through metamorphosis.

Usually the encapsulated veligers would cast off the shell inside the capsule and crawl away as metamorphosed juveniles. However, some veligers from egg masses in full strength and dilute seawater hatched before metamorphosis while others in the same egg mass remained two to three days longer in the capsule and metamorphosed before hatching. We were not able to follow the fate of the

Table 1

Developmental features of two *Elysia chlorotica* populations. All values expressed as mean \pm SD, followed by sample size in parenthesis. * Significant at the 0.01 level; ** 20 veligers observed in one culture only, in all other cases embryos were observed in more than one egg case.

	Ipswich population (encapsulated metamorphosis)	Martha's Vineyard population (planktonic)	<i>t</i> -statistic
Length of field-collected animals	7.60 \pm 2.58 mm (133)	20.01 \pm 8.00 mm (233)	*17.56
Eggs per egg mass	175.67 \pm 112.53 (6)	8901.5 \pm 7257.9 (16)	*2.68
Diameter of egg	96.00 \pm 8.22 μ m (5)	79.33 \pm 2.58 μ m (15)	*7.18
Length of egg capsule	309.00 \pm 8.22 μ m (5)	164.00 \pm 12.42 μ m (15)	*24.17
Days to veliger after deposition	3.00 \pm 0 (93)	2.88 \pm 0.32 (34)	*3.49
Days to eyespot after deposition	9.00 \pm 0 (93)	**13–15 (20)	—
Days to metamorphosis after deposition	13.83 \pm 8.60 (93)	21.56 \pm 0.50 (34)	*49.18

early hatching veligers. After hatching from the egg masses, juveniles would begin to feed on *Vaucheria* filaments and the previously clear digestive gland turned a dark green color.

Culture of Planktonic Veligers

Developmental characteristics of the population from Martha's Vineyard are also listed in Table 1. Field-collected animals had a mean length of 20.01 mm. The mean number of eggs/egg mass was 8901.5. The mean egg diameter was 79.33 μ m or about half the mean capsule length, which was 164.00 μ m. The egg masses lacked the thick gelatinous layer of the encapsulated metamorphosis type. Embryos reached the veliger stage in approximately three days and developed dorsal black pigment bands before hatching. After hatching on day 7 or 8 following egg mass deposition, veligers spent 14 to 15 days feeding on unicellular algae prior to metamorphosis. Eyespots developed 13 to 15 days after egg mass deposition. As the veligers matured a propodium developed, and just prior to metamorphosis the black pigment band spread to cover much of the dorsal surface of the animal. When the pigmented veligers were presented with filaments of *Vaucheria*, they settled on the algal filament, velum down, with the shell lifted upwards. Metamorphosis took place over a period of one to two days. Occasionally, metamorphosis occurred spontaneously in culture beakers before the veligers were exposed to the algal substrate.

Metamorphosis on Different Algal Substrates

Of the 100 veligers placed in each of the culture dishes with the different algal species, 50 to 60 metamorphosed in the dishes containing either *Vaucheria compacta* or *V. litorea*. Only one metamorphosed juvenile was found in either of the culture dishes containing *Enteromorpha* or *Bryopsis*.

Statistical Comparison of the Two Populations

The results of the two-tailed "Student's" *t*-tests comparing the developmental characteristics of the two populations are listed in Table 1. For all developmental characteristics compared there was a statistically significant difference between the two populations ($P \leq 0.01$).

Laboratory Crosses—Parental, F₁, and F₂ Generations

Egg capsule length and shell length at hatching: Figure 1 shows the distribution of egg capsule lengths and shell lengths at hatching measured from egg masses deposited by the parental, F₁, and F₂ generations. The F₁ generation consisted of a total of 25 morphologically Ipswich-type egg masses (Ipswich F₁) and 34 morphologically Martha's Vineyard-type egg masses (Martha's Vineyard F₁). Figure 1 illustrates that both capsule length and shell length of the F₁ egg masses were distributed bimodally; each set of measurements corresponded closely to those of the similar parental generation.

Table 2

Developmental features of *Elysia chlorotica* (Ipswich population) at two salinities. All values expressed as mean \pm SD, followed by sample size in parenthesis. * Significant at the 0.01 level.

	Salinity at 33‰	Salinity at 17‰	<i>t</i> -statistic
Days to veliger after deposition	3.00 \pm 0 (93)	2.33 \pm 0.49 (12)	*13.51
Days to eyespot after deposition	9.00 \pm 0 (93)	5.92 \pm 0.29 (12)	*106.55
Days to metamorphosis after deposition	13.83 \pm 0.86 (93)	9.25 \pm 0.87 (12)	*17.21

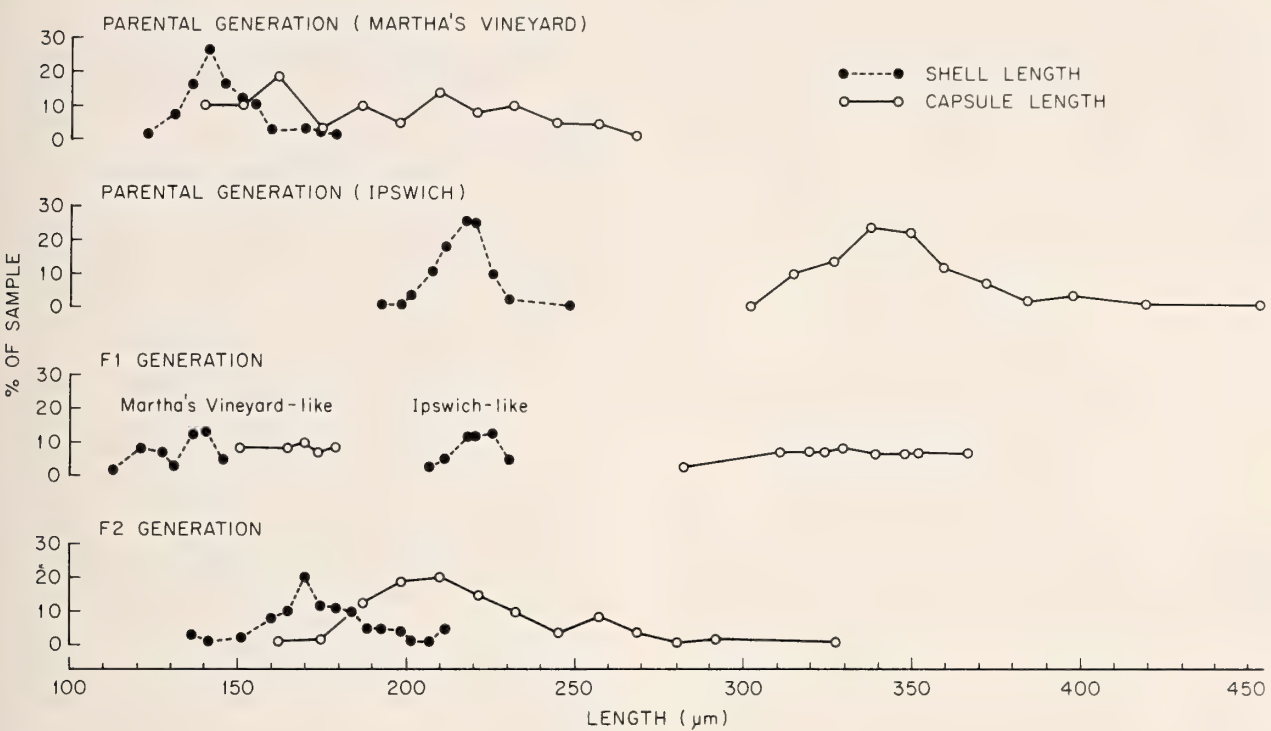


Figure 1

Relationship between shell length (μm) at hatching and egg capsule length (μm) for each population. Note especially the bimodal distributions of shell and capsule lengths in the F₁ generation and convergence of these characters in the F₂ generation.

In contrast to the F₁ egg masses, the 48 F₂ egg masses could not be classified as either Ipswich-type or Martha's Vineyard-type. Both capsule length and shell length at hatching are distributed unimodally (Figure 1), with the means falling between those of the parental and F₁ generations (Table 3). In all generations, egg capsule sizes were more variable than shell lengths.

Egg capsule lengths and shell lengths for all five populations combined were highly significantly different when analyzed using one-way ANOVA for unequal sample sizes (SNEDECOR & COCHRAN, 1967) ($F_{4,355} = 3027.3$, $P \leq 0.01$ for capsules; $F_{4,355} = 200.4$, $P \leq 0.01$ for shells). Subse-

quent application of the Newman-Keuls modification of the Q-test for significant differences between means showed that F₂ capsule lengths and shell lengths differed significantly from those of both the Martha's Vineyard F₁ and Ipswich F₁ populations ($D = 11.1 \mu\text{m}$ for shells, $P \leq 0.05$; $D = 20.9 \mu\text{m}$ for capsules, $P \leq 0.05$; and Figure 2). The Martha's Vineyard F₁ and parental generations also differed significantly, but the Ipswich F₁ and the Ipswich parental generations did not (Figure 2).

Hatching and metamorphosis: Table 4 lists the developmental stage at hatching and the time from egg mass

Table 3

Laboratory crosses of *Elysia chlorotica*: egg capsule length and shell length per generation. All values expressed as mean \pm SD, followed by sample size in parenthesis.

Generation	Capsule length (μm)	Shell length (μm)
Parental—Martha's Vineyard	192.1 \pm 36.3 (100)	145.8 \pm 10.6 (80)
Parental—Ipswich	348.8 \pm 24.3 (100)	216.7 \pm 7.9 (100)
F ₁ —Martha's Vineyard-type	167.2 \pm 10.2 (30)	134.1 \pm 8.7 (30)
F ₁ —Ipswich-type	330.6 \pm 23.8 (30)	220.6 \pm 6.6 (30)
F ₂	219.3 \pm 28.9 (100)	176.5 \pm 16.2 (100)

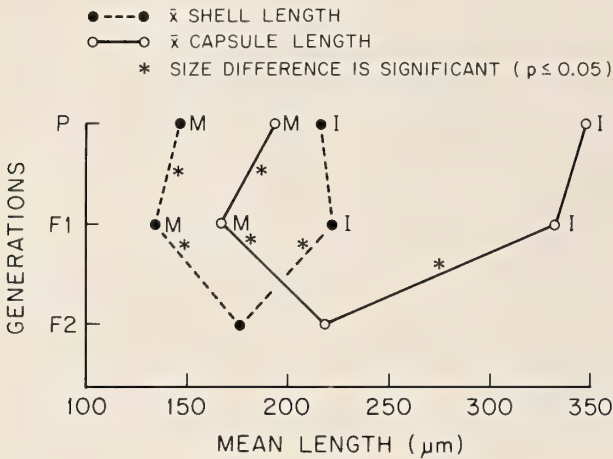


Figure 2

Mean shell and capsule lengths per generation; asterisk indicates means significantly different at $P \leq 0.05$. P, parental generation; F₁, first generation; F₂, second generation; M, Martha's Vineyard (P) or Martha's Vineyard-like (F₁) population; I, Ipswich (P) or Ipswich-like (F₁) population.

deposition to hatching for each population. The trend in the crosses is toward reduction of time spent in intracapsular development and the production of planktotrophic veligers. Although the F₂ veligers are significantly larger than the Martha's Vineyard parental veligers (Table 3 and Figure 2), they hatch in about the same amount of time—five to seven days for the Martha's Vineyard generation *versus* five to nine days for the F₂ generation (Table 4). The F₂ veligers also differ from the Martha's Vineyard parental veligers because eyespots are found in a variable fraction of the hatchlings from each egg mass.

The days from egg mass deposition to hatching were significantly different overall for the F₁ and F₂ populations

($F_{2,57} = 105.6$, $P \leq 0.01$). By the Newman-Keuls Q-test, the number of days to hatching in the F₂ generation, which appears intermediate in time between the Martha's Vineyard and Ipswich F₁ populations, differed significantly from days to hatching of both the Martha's Vineyard-type F₁ and Ipswich-type F₁ populations ($D = 0.2$ days, $P \leq 0.05$; and Table 4).

Self-fertilization and control crosses: Some of the newly metamorphosed individuals that were isolated from parental egg masses did lay egg masses. However, development of eggs in these egg masses was abnormal in both populations and no juveniles were produced.

All F₁ and F₂ egg masses produced by intrapopulation crosses (Ipswich \times Ipswich and Martha's Vineyard \times Martha's Vineyard) were of the parental developmental type. That is, F₂ egg masses laid in the Ipswich crosses had large capsules and most juveniles hatched from egg capsules following metamorphosis; F₂ egg masses laid by the Martha's Vineyard crosses had small capsules and hatched as veligers without eyespots.

DISCUSSION

Compared to other opisthobranchs, *Elysia chlorotica* is cultured with relative ease. First, the culture of direct developers is simple compared to planktonic developers because they do not require unicellular algae for growth and special techniques to change culture water. Also, in this study, normal development of direct developers took place even with a significant change in salinity.

Although it is more difficult to feed and clean them, the planktotrophic veligers of this species have a short planktonic stage when compared with 34 to 40 days in other opisthobranchs (SWITZER-DUNLAP & HADFIELD, 1977; HARRIGAN & ALKON, 1978b; CHIA & KOSS, 1978). The key to the successful culture of the planktonic veligers is the identification of the substrate for metamorphosis, in

Table 4

Laboratory crosses of *Elysia chlorotica*: developmental stage at hatching and time to hatching in each generation.

Generation	Egg masses/ gener- ation	Hatching stage	Days to hatching after deposition (mean \pm SD)
Parental—Martha's Vineyard	10	100% veligers (no eyespots, no propodium)	5.8 \pm 1.0
Parental—Ipswich	10	100% juveniles	10.67 \pm 0.5
F ₁ —Martha's Vineyard-type	34	100% veligers (no eyespots, no propodium)	5.2 \pm 0.8
F ₁ —Ipswich-type	25	27% veligers with eyespots and propodium; 59% mixed veligers and juveniles; 17% juveniles only	10.2 \pm 2.0
F ₂	48	100% veligers, some with eyespots and propodium	7.0 \pm 0.8

this case, *Vaucheria*. It is not surprising that *Vaucheria* is the substrate for metamorphosis because adult digestive cells contain symbiotic chloroplasts which originate from *Vaucheria* (GRAVES *et al.*, 1979; WEST, 1979).

There are two important differences between direct development and planktotrophic development among opisthobranch species. First, in the direct development of any species, veligers require a stored food source because they do not feed on unicellular algae. Food reserves are stored as yolk in the egg. Consequently, opisthobranchs with direct development usually have large eggs, ranging from 205 to 400 μm in diameter (THOMPSON, 1967, 1976). Although the population with direct development in this study has a larger egg size than the population with planktotrophic veligers, the average diameter is only 96 μm . It is possible that food reserves may be stored in extraembryonic albumen in addition to yolk, which could account for the large capsule size in the direct developers. CLARK & JENSEN (1981) have proposed that large capsules and extraembryonic nutrients are typical of direct development in all ascoglossans.

A second difference accompanying direct development is that encapsulated metamorphosis takes place without external cues (BONAR, 1978). Models of metamorphosis of planktonic larvae involve some precise chemical cue which triggers a neuronal response in mature veligers (HADFIELD, 1978). Differences between Ipswich and Martha's Vineyard veligers could present an interesting problem in developmental neurobiology. It may be significant that both the present study and the study by HARRIGAN & ALKON (1978a) found that not all Martha's Vineyard veligers required *Vaucheria* for metamorphosis. If planktonic development was the original development type of the species, it could be that populations with encapsulated metamorphosis developed from the certain percentage of all veligers which could metamorphose without external cue.

There are two other species of opisthobranch where the existence of more than one developmental pattern in the species is described in some detail. In the case of both *Tenellia pallida* (Alder & Hancock) (EYSTER, 1979) and the ascoglossan *Elysia cauze* (Marcus, 1957) (CLARK *et al.*, 1979) the two developmental patterns appeared to occur within single populations. For *E. cauze* the patterns were separated on a seasonal basis and no laboratory crosses were done. In the case of *T. pallida*, crosses were made by pairing field-collected individuals of unknown reproductive type. All F_1 offspring were not intermediate in character but were of one or the other developmental type in the population. This is similar to the parental type F_1 generation in our study of *Elysia chlorotica*. Unfortunately, in the *T. pallida* study no F_2 generation was produced.

The results of the hybridization of the two *Elysia chlorotica* populations were unexpected. The continuous distribution of capsule length and shell length in the F_2 gen-

eration suggests that these characters are controlled by multiple genes. However, this type of distribution is usually expected for the F_1 hybrid generation not the F_2 generation (FALCONER, 1960). Two possible explanations for these results are: (1) the control of certain developmental traits by maternal genes and (2) self-fertilization.

In the case of maternal control it is possible that the morphology of F_1 and F_2 egg capsules depends on the maternal genotype regardless of the genotype of egg and veliger. This model would account for the appearance of Ipswich-type and Martha's Vineyard-type capsules in the F_1 generation because they were deposited by nonhybrid parents, and intermediate or hybrid capsule types in the F_2 generation because they were deposited by hybrid parents. Based on this argument it is more difficult to explain why hatching time is intermediate in the F_2 and not in the F_1 generation. In the case of opisthobranchs, hatching from egg masses is thought to depend on the production of some enzyme by the veliger (DAVIS, 1968). If this is the case, hatching should depend on veliger genotype. However, it is possible that a maternal control of food reserves in egg yolk or capsule albumen, as well as a maternal control of capsule structure, could influence when veligers hatch.

The persistence of parental characters in the F_1 generation also could be explained either by selfing in the parental generation while the F_1 outcrossed or by selfing in both the parental and F_1 generations with an eventual breakdown of parental characters in the F_2 generation. There is one report of self-fertilization in another ascoglossan (KAWAGUTI & YAMASU, 1961). However, because in our laboratory cultures, egg masses laid by isolated individuals developed abnormally, it seems that self-fertilization alone could not explain the maintenance of maternal characters in the F_1 generation.

The production of viable F_1 and F_2 offspring from the crosses does not prove that the two populations are actually one species. More extensive genetic studies would have to be performed to determine whether these populations actually represent one species. However, the results do suggest that crosses between populations could occur in the field and that other populations could exhibit developmental characteristics different from the Ipswich or Martha's Vineyard populations. So far, descriptions of reproductive variation of *Elysia chlorotica* are limited to the two geographically separated populations in this study. It is not known whether populations with the characteristics of the F_1 and F_2 generations of this study occur naturally. Although *E. chlorotica* has a geographic range from Nova Scotia to Florida (MARCUS, 1980), descriptions of development in other populations are limited to one report describing planktotrophic development in Chesapeake Bay and Virginia (VOGEL, 1978). Further studies are underway to identify the extent of variation in other populations and to find whether any correlations exist between certain habitats and development types.

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The Opisthobranch Mollusks of Humboldt County, California

by

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Abstract. Sixty-eight species of opisthobranch Mollusca are documented from twenty-one collection sites in Humboldt County, California. The sighting of *Hancockia californica* represents a geographical range extension. Aspects of the biology of certain species are discussed.

INTRODUCTION

SINCE 1968, MANY annotated checklists and natural history reports discussing the opisthobranch gastropods from California counties and other geographical localities have been published (SPHON & LANCE, 1968; ROLLER & LONG, 1969; ROLLER, 1970b; GOSLINER & WILLIAMS, 1970, 1973b; BERTSCH *et al.*, 1972; HOLLEMAN, 1972; GODDARD, 1973; BEHRENS & TUEL, 1977; NYBAKKEN, 1978; BEHRENS, 1980b). From these reports, our knowledge of these mollusks has increased greatly, but none of these works examines the opisthobranch fauna from areas north of Marin County, California (latitude 38°17'38"N; longitude 123°00'05"W). As a result, the opisthobranch fauna of northern California is poorly documented and the number of publications dealing specifically with the opisthobranch gastropods of Humboldt County is extremely limited. WICKSTEN & DEMARTINI (1973) described a new anthozoan prey species of the dendronotacean nudibranch *Tochuina tetraquetra* (Pallas, 1788) from Trinidad Bay; McDONALD (1977) noted a photograph of *Crimora coneja* Marcus, 1961, reportedly from Humboldt County; and JAECKLE (1981a, b) reported geographical range extensions for several nudibranch species. Three marine biota surveys have been conducted in certain littoral and sublittoral localities in Humboldt County (BOYD & DEMARTINI, 1977; BOYD, 1979; BOYD & SJOGREN, 1979), and these list the opisthobranch species from their respective areas.

This paper presents the results of a three-year examination of the gastropod subclass Opisthobranchia in Humboldt County and a compilation of data from previously published works. Personal sightings have been augmented by specimens collected by the faculty and graduate students of the Department of Biological Sciences, Humboldt State University, Arcata, California.

Humboldt County (Figure 1) is located in northwestern California, and the coastline is characterized by rocky cliffs, expanses of rocky littoral areas, sandy beaches, and one major estuary, Humboldt Bay. A total of 57 collection trips, primarily during the months of June, July and August, were made at 14 collection sites; specimens supplied from additional localities and previously published accounts bring the cumulative total to 21 collection sites (Table 1; Figure 1). Topographically, these sites range from an area of extreme oceanic exposure (*e.g.*, North Jetty) through semi-protected rocky habitats (*e.g.*, Trinidad Bay) to calm, floating dock communities and *Zostera marina* beds of Humboldt Bay (*i.e.*, Fields Landing and the Samoa Boat Ramp).

OCCURRENCE AND DISCUSSION OF HUMBOLDT COUNTY OPISTHOBRANCH MOLLUSKS

Except where noted, all examined specimens were collected from littoral localities. In only one instance was bathymetric data obtained for specimens collected in sublittoral areas, denoted by an (s). The sites of collection are keyed by numbers (Table 1) with each individual species in the list below. An asterisk (*) denotes a geographical range extension; a (+) indicates that the collection data were obtained from the Humboldt State University marine invertebrate museum collection.

CEPHALASPIDEA

ACTEONIDAE

Rictaxis punctocaelatus (Carpenter, 1864)
7, 15.

AGLAJIDAE

Aglaja ocelligera (Bergh, 1894)+
8(s).

Melanochlamys diomedea (Bergh, 1894)+
8(s).

ANASPIDEA

APLYSIIDAE

Aplysia californica Cooper, 1863

Aplysia californica is reportedly very common in the discharge canal of the Humboldt Bay Power Plant (David Behrens, Pacific Gas & Electric Company, personal communication); however, no specimens were sighted during this study.

Phyllaplysia taylori Dall, 1900

13, 17. *Phyllaplysia taylori* is commonly epiphytic on the marine angiosperm *Zostera marina* Linnaeus in Humboldt Bay. Nidosomes of *P. taylori* have been found on *Zostera* from May through October and young specimens are common in October and November.

NOTASPIDEA

PLEUROBRANCHIDAE

Berthella californica (Dall, 1900)

3, 4. Many members of the notaspidean family Pleurobranchidae are known to produce epidermal acidic secretions as an active defense mechanism (THOMPSON, 1976a). A field observation suggests that *Berthella californica* has the capacity to secrete a repellent material. At Palmer's Point (#4), a specimen of the carnivorous asteroid *Pycnopodia helianthoides* (Brandt, 1835) was observed crawling onto a specimen of *B. californica*. After approximately a 30-second time interval, the *Pycnopodia* specimen moved rapidly away from the pleurobranch. An examination of the area immediately following this interaction revealed no other organisms that could conceivably have elicited this response by the asteroid.

Pleurobranchaea californica MacFarland, 1966

19(s). One specimen collected by a commercial fisherman at 550 m depth.

SACOGLOSSA

STILIGERIDAE

Alderia modesta (Lovén, 1844)
9, 10, 11.

Aplysiopsis smithi (Marcus, 1961)

5. This sacoglossan species was feeding on an unidentified filamentous chlorophyte in a small supralittoral fringe tidal pool. Among the algal filaments were numerous nidosomes of *A. smithi* (shape of nidosome described by GONOR, 1961).

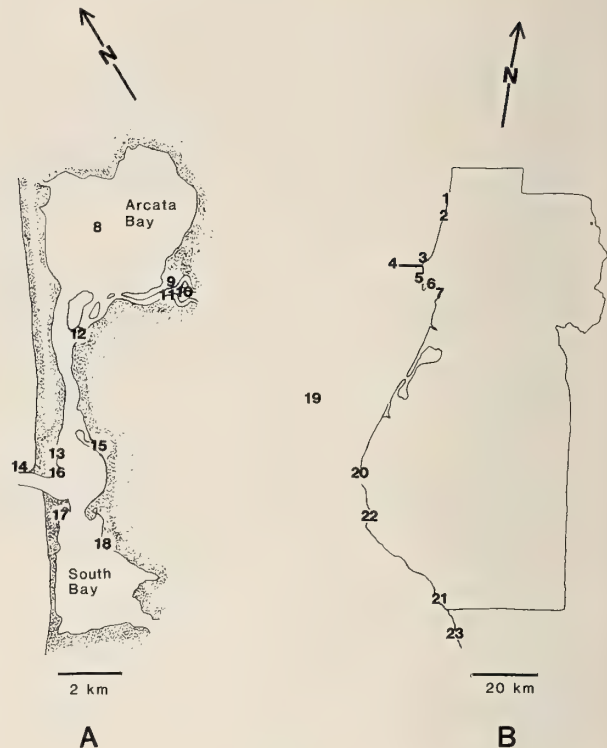


Figure 1

Humboldt County, California. Numbers indicate sites of collection (see text). A. Humboldt Bay; B. Humboldt County.

Placida dendritica (Alder & Hancock, 1843)
3, 6.

Stiliger fuscovittatus Lance, 1962
8.

NUDIBRANCHIA

Doridacea

OKENIIDAE

Ancula pacifica MacFarland, 1905
3, 4, 16.

Hopkinsia rosacea MacFarland, 1905

4. A single specimen of this suctorian dorid was found on its prey, the bryozoan *Eurystomella bilabiata* (Hincks, 1884) (McBETH, 1971). The dorsal papillae of *H. rosacea* are reportedly tall, slender, and simple (BEEMAN & WILLIAMS, 1980; BEHRENS, 1980a; McDONALD & NYBAKKEN, 1980); however, many of this specimen's papillae were branched and/or apically bifurcated as described by MACFARLAND (1906).

ONCHIDORIDIDAE

Acanthodoris nanaimoensis O'Donoghue, 1921
1-2, 4, 6, 6(s), 16.

Table 1
Geographical localities.

		Latitude	Longitude
1-2	Redwood National Park	41°16'10"N	124°06'35"W
			to
		41°22'41"N	125°04'12"W
3	Palmer's Point	41°07'21"N	124°09'32"W
4	Abalone Beach	41°07'20"N	124°09'32"W
5	Omenoku Point	41°04'01"N	124°09'19"W
6	Trinidad Bay	41°03'07"N	124°07'51"W
7	Luffenholtz Beach	41°02'51"N	124°07'04"W
8	Arcata Bay, Humboldt Bay (=North Bay of JAECKLE, 1981b)	~40°51'N	~124°08'W
9	Freshwater Slough	40°48'17"N	124°07'W
10	Park Street Marsh	40°48'17"N	124°07'W
11	Park Street Slough	40°48'17"N	124°07'W
12	Eureka Boat Harbor	40°48'15"N	124°10'41"W
13	Somoa Boat Ramp	40°46'21"N	124°18'39"W
14	North Jetty	40°46'09"N	124°14'15"W
15	Elk River Slough	40°46'00"N	124°11'57"W
16	Humboldt Bay Coast Guard Station (HBCGS)	40°45'55"N	124°13'04"W
17	South Spit, South Bay, Humboldt Bay	40°44'00"N	124°12'31"W
18	Fields Landing	40°43'26"N	124°13'20"W
19	Eel River Submarine Canyon	~40°41'N	~124°40'W
20	Cape Mendocino	40°26'44"N	124°24'43"W
21	Point Delgada	40°01'27"N	124°04'17"W
22-23	King Range	40°19'38"N	124°20'14"W
			to
		39°59'38"N	123°59'46"W

Acanthodoris rhodoceras Cockerell in Cockerell & Eliot, 1905

16.

Adalaria sp.

16. The radular and external morphology of this onchidorididean species correspond with that of *Adalaria* sp. (BEHRENS, 1980a, fig. 138) and to a specimen supplied by Sandra Millen (University of British Columbia). The orange ground color of the specimens collected in Humboldt County differs significantly from the white coloration of northern forms. This species is found exclusively on the orange anascan cheilostome bryozoan *Lyrula hippocrepis* (Hincks, 1882), upon which it feeds. Nidosomes, deposited directly on *Lyrula*, have been found in August and October.

Onchidoris bilamellata (Linnaeus, 1767)

3, 4, 6(s), 16. This species was sighted on or near the barnacles *Balanus crenatus* Bruguire, 1789, or *B. glandula* Darwin, 1854. Nidosomes were found in littoral areas in January and July; a large sublittoral population in Trinidad Bay spawns in late summer (Tim Stebbins, University of Southern California, personal communication). HURST (1967) reported that nidosomes of *O. bilamellata* are extremely common in Washington during the winter months.

Onchidoris hystricina (Bergh, 1878)

3, 4, 6, 14, 16.

Onchidoris muricata (Müller, 1776)

4, 6, 16.

TRIOPHIDAE

Triopha catalinae (Cooper, 1863)

3, 4, 6, 6(s).

Triopha maculata MacFarland, 1905

3, 4, 6, 16.

Crimora coneja Marcus, 1961

This species was not sighted during the study; however, McDONALD (1977) noted a photograph of *Crimora coneja* reportedly from Humboldt County.

Aegires albopunctatus MacFarland, 1905

3, 4, 6(s).

Laila cockerelli MacFarland, 1905

4.

POLYCERIDAE

Polycera atra MacFarland, 1905

8.

Polycera zosterae O'Donoghue, 1924

14. On the bryozoan *Dendrobeania laxa* (Robertson, 1905).

CADLINIDAE

Cadlina flavomaculata MacFarland, 1905
4.

Cadlina luteomarginata MacFarland, 1905
3, 4, 6, 6(s), 16.

Cadlina modesta MacFarland, 1966
4.

ACTINOCYCLIDAE

Hallaxa chani Gosliner & Williams, 1975
3, 4.

ALDISIDAE

Aldisa cooperi Robilliard & Baba, 1972
6.

Aldisa sanguinea (Cooper, 1863)
3.

ROSTANGIDAE

Rostanga pulchra MacFarland, 1905
1-2, 3, 4, 6, 6(s), 16, 22-23.

ARCHIDORIDIDAE

Archidoris montereyensis (Cooper, 1863)

1-2, 3, 4, 6, 6(s), 12, 16, 17. Specimens sighted in rocky littoral areas possessed the typical yellow to orange ground color with scattered black notal pigmentation. However, individuals examined from soft bottom areas of Humboldt Bay exhibited a dark yellow-brown to dark gray ground coloration. In several instances, the ground coloration was sufficiently dark to nearly obscure the black notal pigmentation.

Archidoris montereyensis has been seen feeding on the sponge *Halichondria panicea* (Pallas, 1766).

Archidoris odhneri (MacFarland, 1966)
6, 6(s).

DISCODORIDIDAE

Anisodoris nobilis (MacFarland, 1905)
3, 4, 6, 6(s), 16.

Diaulula sandiegensis (Cooper, 1863)
1-2, 3, 4, 6, 6(s), 14, 16, 22-23.

Discodoris heathi MacFarland, 1905
3.

DENDRODORIDIDAE

Doriopsilla albopunctata (Cooper, 1863)
4, 21.

Dendronotacea

TRITONIIDAE

Tritonia diomedea Bergh, 1894
6(s).

Tritonia festiva (Stearns, 1873)

1-2, 3, 4, 16, 21. In Humboldt County, *Tritonia festiva* exhibits two distinct coloration patterns. The dominant phase consists of the typical white ground color with a dorsal, reticulating, opaque white line network; a series of middorsal, oval pink spots is present on some individuals. Specimens collected at the HBCGS (#16) exhibited the alternate coloration, a translucent light pink ground color with little or no evidence of a dorsal, white line network. At this study site, a population of the pink alcyonacean octocoral *Gersemia rubiformis* (Pallas, 1788) exists and *T. festiva* preys on this anthozoan. The pink coloration of *Tritonia* does not appear to be restricted to the digestive tract as reported by GOMEZ (1973) for specimens of *T. festiva* feeding on *Lophogorgia chilensis* (Verrill, 1868). The feeding behavior differs from previously published accounts of tritonid feeding (GOMEZ, 1973; THOMPSON, 1976a). When *Tritonia* comes in contact with a *Gersemia* colony, the predator's oral veil expands laterally and the specimen lunges into the alcyonacean colony. The pink anthozoan tissue can be observed passing through the buccal mass into the esophagus. The calcareous spicules of *Gersemia* are present in the fecal pellets of pink specimens of *Tritonia*.

The utilization of *Gersemia rubiformis* as a prey item by *T. festiva* contradicts NYBAKKEN & MACDONALD (1981) who state "the unusually narrow radula of *T. festiva* seems to correlate with the prey" (in that case *Clavularia* sp.).

Tochuina tetraquetra (Pallas, 1788)
6, 6(s).

HANCOCKIIDAE

Hancockia californica MacFarland, 1923*

6. This species was found exclusively on the rhodophyte *Polysiphonia* sp. attached to wharf pilings at this study site.

The sighting of *Hancockia californica* in Humboldt County represents a geographical range extension. The previous northernmost occurrence of *H. californica* was Dillon Beach, Marin County, California (McDONALD & NYBAKKEN, 1980).

DENDRONOTIDAE

Dendronotus diversicolor Robilliard, 1970
6.

Dendronotus frondosus (Ascanius, 1774)
1-2, 3, 4, 6, 6(s), 12, 13, 16, 17, 18, 22-23.

Dendronotus iris Cooper, 1863
15.

Dendronotus subramosus MacFarland, 1966

3, 4, 6, 16. Observed feeding on the hydroids *Obelia* sp. and *Tubularia marina* (Torrey, 1902).

Table 2
Hydrozoan prey species of *Hermisenda crassicornis*.

Anthomedusae	Leptomedusae	Chondrophora
<i>Eudendrium californicum</i>	<i>Abietinaria abietina</i> (Linnaeus, 1758)	<i>Verella velella</i> Linnaeus, 1758
<i>Eudendrium rameum</i> (Linnaeus, 1758)	<i>Abietinaria greenei</i> (Murray, 1860)	
<i>Stauridiosarsia japonica</i> (Nagao, 1962)	<i>Campanularia ritteri</i> Nutting, 1901	
<i>Tubularia crocea</i>	<i>Halecium corrugatum</i> Nutting, 1899	
<i>Tubularia marina</i>	<i>Obelia dichotoma</i>	
<i>Polyorchis</i> sp.	<i>Sertularella conica</i> Allman, 1877	

DOTIDAE

Doto amyra Marcus, 1961

1-2, 6. Although no specimens definitely assignable to *Doto amyra* were sighted during this study, BOYD & DEMARTINI (1977) and BOYD (1979) have reported this species from Humboldt County.

Doto columbiana O'Donoghue, 1921

12. Feeding on *Obelia* sp.

Doto kya Marcus, 1961

3, 4, 12, 16. ROLLER's (1970a) and McDONALD's (1975, 1977) work on the five species of *Doto* described by MARCUS (1961) and MACFARLAND (1966) resulted in the three currently recognized species of this genus in the northeast Pacific: *Doto amyra*, *D. columbiana*, and *D. kya*. However, McDONALD (1977) commented on the continued taxonomic confusion surrounding these five species, and BEEMAN & WILLIAMS (1980) reported on the difficulty of species identification. Specimens have been collected in Humboldt County which are morphologically identical to MARCUS' (1961) description of *D. amyra*, but the presence and distribution of black pigmentation on the cerata and dorsum indicate that these specimens are representatives of *D. kya*. Systematic revision is clearly needed.

Doto kya possesses a varied diet, utilizing *Abietinaria* sp., *Aglaophenia struthionides* (Murray, 1860), *Eudendrium californicum*, *Obelia dichotoma* (Linnaeus, 1758), *Plumularia* sp., and *Sertularella* sp. as prey. Nidosomes of *Doto* spp. have been found throughout the year in the hydrorhizal area of all species, except *E. californicum*.

Arminacea

ARMINIDAE

Armina californica (Cooper, 1863)

4. Although typically found on sandy mud bottoms (McDONALD & NYBAKKEN, 1980) in association with *Renilla* spp. and *Ptilosarcus gurneyi* (Gray, 1860) (MACFARLAND, 1966; McDONALD, 1977), the single specimen collected in Humboldt County was found in a rocky littoral habitat with no evidence of pennatulacean prey species in the area of collection.

This specimen's coloration deviated significantly from normal pigmentation patterns described for *Armina californica*. The dorsum was completely white with no evidence of light pinkish-brown or cream pigmentation.

DIRONIDAE

Dirona albolineata MacFarland in Cockerell & Eliot, 1905

1-2, 4, 6, 6(s), 14, 16, 22-23.

Dirona picta MacFarland in Cockerell & Eliot, 1905

1-2, 3, 4, 6, 14, 16, 22-23.

JANOLIDAE

Janolus fuscus O'Donoghue, 1924

3, 4, 6, 13, 16, 22-23.

Aeolidacea

FLABELLINIDAE

Flabellina iodinea (Cooper, 1863)

6(s).

Flabellina pricei (MacFarland, 1966)

1-2, 6. No specimens of this species were sighted during this study; however, BOYD & DEMARTINI (1977) and BOYD (1979) reported *Flabellina pricei* from Humboldt County.

Flabellina trilineata (O'Donoghue, 1921)

1-2, 4, 5, 6, 13, 16.

EUBRANCHIDAE

Cumanotus beaumonti (Eliot, 1906)

17. When disturbed, the cerata of the examined specimen moved in a coordinated dorso-ventral fashion; THOMPSON (1976b) depicts this defensive swimming behavior.

Eubranchus rustyus (Marcus, 1961)

3, 4, 6, 12, 16.

TERGIPEDIDAE

Cuthona abronia (MacFarland, 1966)

4.

Cuthona albocrusta (MacFarland, 1966)

3, 4, 6, 13.

Cuthona cocoachroma Williams & Gosliner, 1979
6, 16.

Cuthona columbiana (O'Donoghue, 1922)
3, 6.

Cuthona divae (Marcus, 1961)
3, 4, 6, 16. In Humboldt County, this species is invariably found in close association with its food source *Hydractinia milleri* Torrey, 1902 (McDONALD & NYBAKKEN, 1980). Numerous pink nidosomes have been found on the perisarc of *H. milleri*, presumably deposited by adjacent specimens of *C. divae*. The deep pink ceratal coloration of these specimens is probably attributable to ingested *H. milleri* polyps.

Cuthona flavovulta (MacFarland, 1966)
3, 4, 6.

Cuthona lagunae (O'Donoghue, 1926)
3, 4, 6.

FACELINIDAE

Hermisenda crassicornis (Eschscholtz, 1831)
1-2, 3, 4, 6, 6(s), 8, 12, 13, 14, 16, 17, 18, 22-23. In terms of abundance and geographical distribution, *Hermisenda crassicornis* is the dominant littoral opisthobranch in Humboldt County. During this study, *H. crassicornis* has been observed feeding on numerous hydrozoan species (Table 2).

AEOLIDIIDAE

Aeolidia papillosa (Linnaeus, 1761)
1-2, 3, 4, 6, 12, 14, 16, 20.

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Doridacean Nudibranchs from Sri Lanka, with Descriptions of Four New Species

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Abstract. Eight doridacean nudibranchs from northeastern Sri Lanka are described and illustrated. Of these, two chromodorids, *Chromodoris conchylata* and *C. adeima*, are new species. Two of the three phyllidiids found also are new to science, *Phyllidia empelia* and *P. alia*. The third, *P. varicosa*, as well as *Gymnodoris citrina* are new records for Sri Lanka.

INTRODUCTION

THE MAJORITY OF observations on the opisthobranch mollusks of the Indian Ocean have been concentrated along the east coast of Africa: EDMUNDS (1971) described the Doridacea from Tanzania and sixteen opisthobranch mollusks from the Seychelles, Tanzania, and the Congo (EDMUNDS, 1972). Rudman worked from eastern Africa across to the tropical West Pacific (RUDMAN, 1977), as well as in the Indo-West Pacific (RUDMAN, 1973, 1982). The Red Sea has furnished a number of scientific collections: one of the first was ELIOT's (1908) collection near Sudan. MARCUS & MARCUS (1959) reported on the Red Sea and the Maldives. GOHAR & ABUL-ELA (1959) studied the development of three Red Sea nudibranchs, and more recently SOLIMAN (1978, 1980) has been working on the biology of Red Sea dorids.

The first records of opisthobranch mollusks from Sri Lanka were published by KELAART (1858, 1859) and were based on collections made in the vicinity of Trincomalee. Walter Elliot collected along the northwestern coast of India during the period 1853-54, accompanying his collection of 41 species with accurate drawings. He sent his drawings and preserved specimens to ALDER & HANCOCK in England, who published their studies in 1864. C. N. E. ELIOT (1906) reviewed these early finds, in addition to FARRAN's (1905) work and BERGH's (1905) extensive collections. Work on Indian and Ceylonese opisthobranchs was thereafter sporadic: ELIOT (1909) added further details of fresh specimens to his previous work on Kelaart's animals; O'DONOGHUE (1932) made notes on 18 species of nudibranchs and ascoglossans from the Gulf of Ma-

naar; WINCKWORTH (1946) wrote on five species of chromodorids he found in Bombay. More recently, BURN (1970) has drawn attention to the Phyllidiidae in redescribing the rare *Phyllidia zeylanica*, rediscovered after almost 100 years in the Gulf of Kutch, western India.

The opportunity arose while visiting Sri Lanka during the summer of 1981 to initiate a new investigation into the opisthobranch Mollusca and their habitats in the region of Trincomalee, the site of Kelaart's first collection of opisthobranchs in Ceylon.

Sri Lanka is a large island, approximately 65,600 km² in area, situated in the Indian Ocean southeast of Cape Cormorin in India. The city of Trincomalee is located on the northeastern coast, which is characterized by sandy bays enclosed within rocky outcrops, with some well-developed lagoon areas and a few coral islands and bays. This coast is exposed to strong winds during four months of the year, with maxima in January (U.S. NAVY, 1957).

In this investigation, 14 species of opisthobranchs were found, 8 of which belong to the suborder Doridacea. Four are described as new species, two Chromodorididae and two Phyllidiidae. Of the remaining four, two are new records for Sri Lanka, *Gymnodoris citrina* and *Phyllidia varicosa*. *Gymnodoris citrina* is redescribed and the problem of discriminating between *G. bicolor* and *G. citrina* is discussed. New observations are presented on the anatomy and histology of several species.

COLLECTION AND METHODS

All the specimens were collected from three localities north of Trincomalee in relatively shallow water (1-4.5 m): none of the reefs is exposed at low tide. Descriptions, drawings, and color photographs of external features were made from life. Anatomical investigations were made using specimens relaxed in 7% magnesium chloride, pre-

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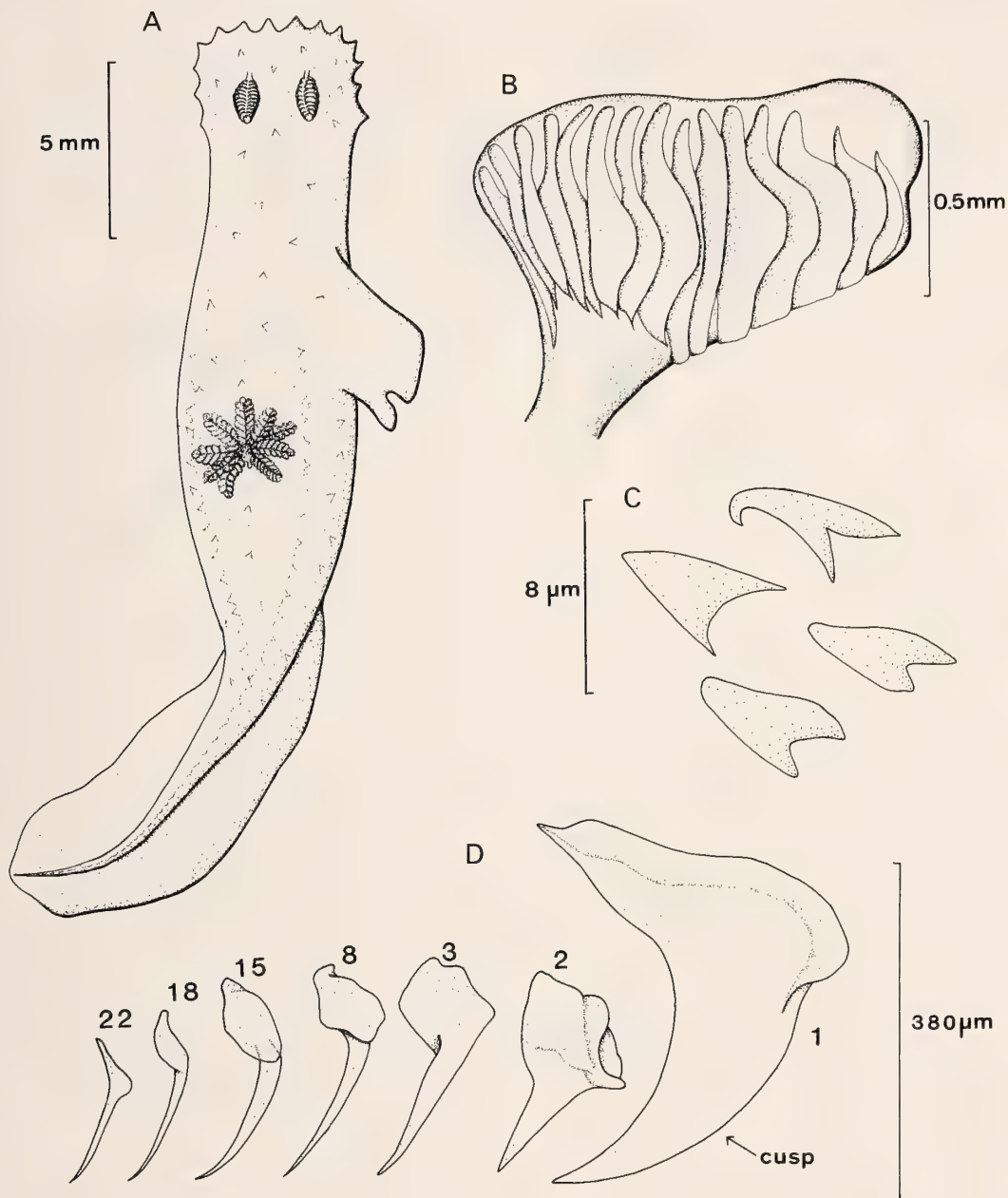


Figure 1

Gymnodoris citrina A. dorsal aspect; B. side view of the rhinophore; C. penial spines (with aid of camera lucida); D. radular teeth (with aid of camera lucida).

served in 4% formalin, and later transferred into 70% alcohol. Jaw and radula preparations were made by removing the buccal mass, dispersing the flesh in warm caustic soda (NaOH), and mounting in polyvinyl lactophenol with lignin pink. The reproductive organs of the single specimens were not dissected in order to preserve the type specimens as completely as possible after removing the radula.

Holotypes and paratypes of the new species have been lodged in the British Museum (Natural History).

Gymnodoris citrina (Bergh, 1877)

(Figure 1)

Trevelyana citrina BERGH, 1877
Gymnodoris citrina: YOUNG, 1967

Material and locality: One specimen, collected under a rock at a depth of 2 m off Pigeon Island (northeast of Trincomalee), on 26 August 1981.

Description: The specimen was 28 mm long and approximately 5 mm wide. It is milky white with small, orange-yellow, low-pointed papillae scattered over the dorsal surface. It is not bilaterally symmetrical; the enlarged genital papilla (now a tube in the preserved specimen) is located to the right of the midline, anterior to the gills, and the branchiae are to the left of the median. Two rows of orange-yellow pointed papillae form a slightly asymmetrical V-shaped pattern on either side of the branchiae. The dorsal surface of the tail and the genital papilla are free of papillae. The front of the mantle is broadly rounded and bears 14 pointed orange-yellow projections (Figure 1A).

The bulbous rhinophores are darker than the pallial tubercles and distinctive in shape. They each have a thin stalk, 15 vertical lamellae, and a swollen club at the distal end (Figure 1B). The branchiae are 9 in number, set in a crescent shape anterior to the small anal papilla. In life, the gills were translucent white, and retracted after much stimulation.

The radula is broad, with the formula $20 \times 28 \cdot 0 \cdot 28$. There is no median tooth, but the cuticle contains a faintly reticulate substructure. The number of marginals increases towards the growing end. The first marginal tooth is more than twice the size of the second marginal: the largest first marginal measures approximately $300 \mu\text{m}$ in length. Each of these large teeth has a long, narrow root and a long, curved, pointed cusp. Root size in proportion to the cusp diminishes towards the outer edges of the radula. The outermost marginals exhibit abruptly recurved tips (Figure 1D). No recognizable jaws survived caustic treatment.

A squash preparation of the retracted penis shows that there are spines lining the lumen. They take the form of triangular arrowheads, approximately $6.6 \mu\text{m}$ long (Figure 1C).

Remarks: Two similar species of *Gymnodoris* exist and have posed difficulties in identification. *Gymnodoris bicolor* (Alder & Hancock, 1864) and *G. citrina* (Bergh, 1877) have been differentiated by the size of the first marginal tooth relative to body size, by the shape of the second marginal, and by the size difference between the first and second marginals. In *G. bicolor*, the first marginal tooth is small in relation to body length; the shape of the second marginal is elongated and triangular; and the second marginal is only slightly smaller than the first marginal. In *G. citrina*, the first marginal is large relative to body length; the second marginal has an awl-shaped cusp and a broad base; and the second marginal is very much smaller than the first, less than half the size. In my specimen, the ratio between body length and first lateral is intermediate, and the first marginal is more than twice the size of the second marginal.

Other, less ambiguous, characteristics follow. The location of the genital opening relative to the gills differs in both species: in *G. bicolor*, the aperture is posterior (KAY & YOUNG, 1969) and in *G. citrina* anterior (YOUNG, 1967) to the gills. The cirral hooks of *G. bicolor* are $24\text{--}36 \mu\text{m}$ long (KAY & YOUNG, 1969) whereas in *G. citrina* they are an order of magnitude smaller, $7\text{--}8.5 \mu\text{m}$ (YOUNG, 1967). In my specimen they were approximately $6.6 \mu\text{m}$ long. The V-shaped arrangement of papillae on the dorsum also seems to be characteristic of *G. citrina*.

Distributions of *G. bicolor* and *G. citrina* are uncertain because ambiguous radular descriptions and incomplete morphological descriptions have not been sufficient to enable one to distinguish between the two. Certain identifications of *G. citrina* indicate a western Indo-Pacific distribution: Palau Island (BERGH, 1877), Eniwetok Atoll (YOUNG, 1967), and now Sri Lanka.

Chromodoris conchyliata Yonow, spec. nov.

(Figures 2 and 9A, B, C)

Material and locality: One specimen found under dead coral at a depth of 4 m in Koduwakattumalai Bay (35 km north of Trincomalee), on 7 August 1981.

Holotype: BM(NH) 19837 W.

Description: The animal was 15 mm long, with the foot extending beyond the mantle. The anterior and posterior ends of the mantle and the rear of the foot are edged with a milky white band. The anterior part of the mantle is bilobed. The body is pale violet with rounded areas of creamy yellow, and deeper violet and red markings. There are 3 dark violet markings on the dorsum: a V-shape near the front with the ends pointing towards the rhinophores, 2 broad lateral bands converging in the midline anterior to the gills, and an X-shape on the rear of the mantle. These dark violet marks redden in places and follow the contours of bilaterally symmetrical yellow spots (Figure 2A). Ventrally, the head, the simple oral tentacles, and the foot are white. The hyponotum is dark purple in the region that corresponds to the pale violet on the dorsum. Where the edging is white above, it is bright red ventrally, fading into white near the head (Figure 2B).

In lateral view, a longitudinal dark violet line can be seen between the foot and the mantle. The animal is fairly high when observed from this angle (Figure 2D).

The rhinophores are lamellated, colored red with white stalks, and retractile into sheaths (Figure 2C). The gills, 8 simple pinnate structures, are tricolored: the upper half is red, both rachis and pinnae, and the lower half has a pale violet rachis with white pinnae (Figure 2E).

The radular formula of the specimen is $43 \times 33 \cdot 1 \cdot 33$. The median tooth is vestigial. All the teeth have pointed denticulations, and the first tooth on either side of the median has a subsidiary cusp (Figures 2F and 9A). The jaw plates consist of blunt hooked rods, the largest about $2 \mu\text{m}$ long.

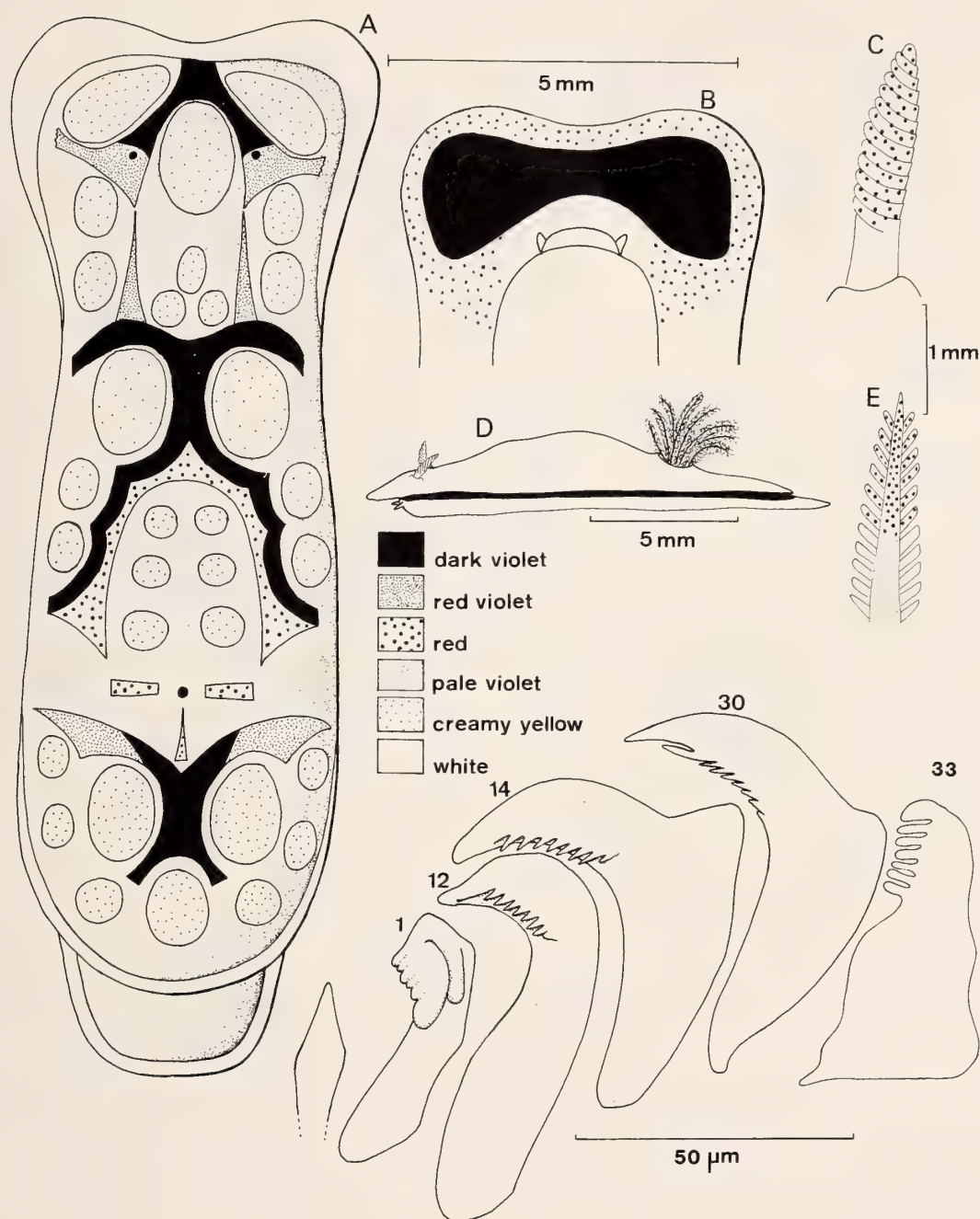


Figure 2

Chromodoris conchylata Yonow, spec. nov. A. dorsal aspect; B. ventral view of the head; C. side view of the rhinophore; D. lateral view; E. gill; F. radular teeth (with aid of camera lucida).

Remarks: This species is distinct from all previously described chromodorids in its color pattern, with 3 distinct sets of dark violet markings on a pale violet body color and the bilobed anterior margin, not a common feature in chromodorids. This species is distinguishable from *Chro-*

modoris geometrica Risbec, 1928, similarly patterned with violet markings. *Chromodoris geometrica* has rays of purple radiating from two parallel median bands (also purple); the rhinophores have white stalks with yellow lamellae; the branchiae are seven in number, each with a yellow

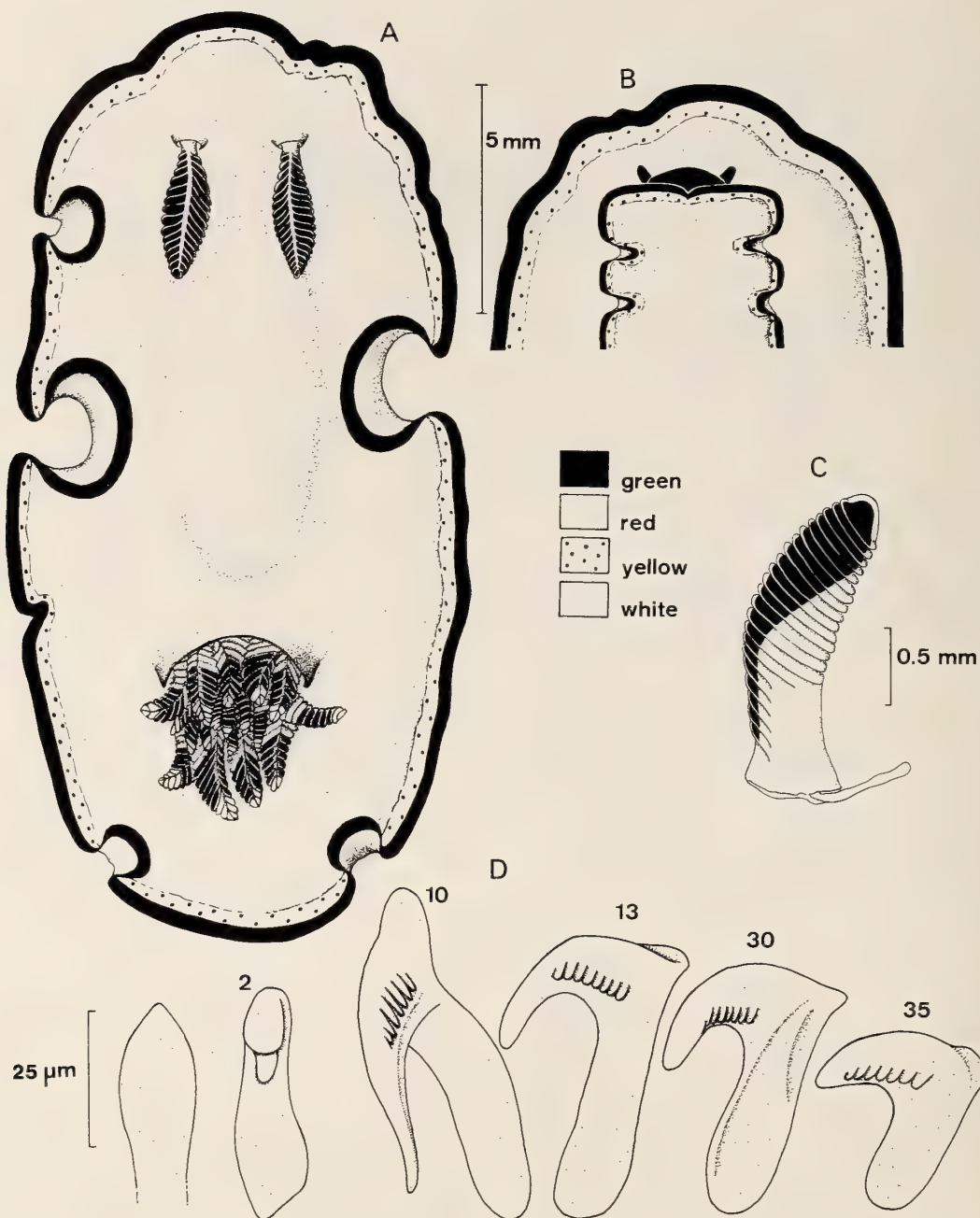


Figure 3

Chromodoris adeima Yonow, spec. nov. A. dorsal aspect; B. ventral view of the head; C. side view of the rhinophore; D. radular teeth (with aid of camera lucida).

rachis and transparent white pinnae (YOUNG, 1967). *Chromodoris geometrica* seems to be limited to the eastern Pacific: New Caledonia (RISBEC, 1928, 1953), New South Wales (ALLAN, 1947) and Eniwetock Atoll (YOUNG, 1967). The radular formulae are similar, as is the form of the teeth. The radula of a 22 mm-long specimen of *C. geo-*

metrica is $43 \times 28.0-28$; the teeth are $53-79 \mu\text{m}$ long and denticulate. The jaw plates consist of simple bifid hooks $32-39 \mu\text{m}$ long (YOUNG, 1967). RUDMAN (1973) also describes *C. cf. geometrica*, a chromodorid with purple reticulations. He states that the color is somewhat variable if the records from New Caledonia, Australia, Eniwetok,

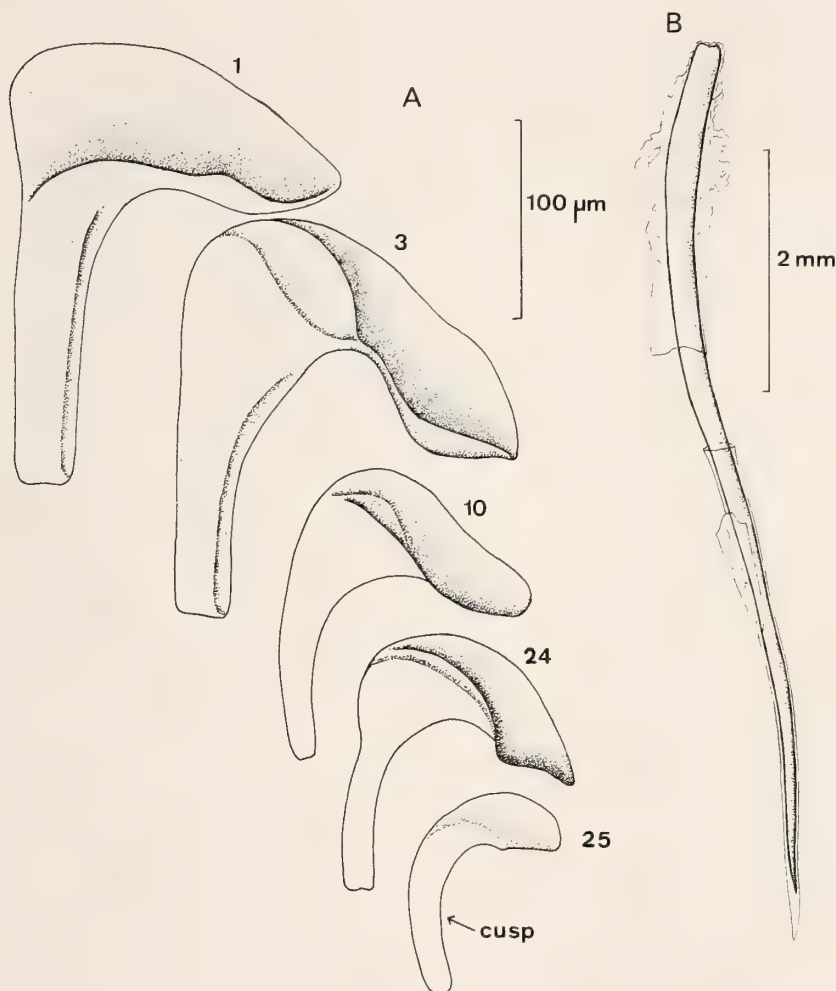


Figure 4

Kentrodonis rubescens A. radular teeth (with aid of camera lucida); B. vestibular stylet (with aid of camera lucida).

and Kenya are of the same species, but that the specimens are linked by (1) the orange-yellow rhinophores (mine were red) and gills (mine were pale violet and white with red), (2) the purple reticulate pattern, and (3) the white yellow pustules. The described specimen probably belongs to the same color group as the above, but is certainly a separate species.

The name *conchyliata* is derived from the Latin *conchyliatus*, meaning "dressed in purple."

Chromodoris adeima Yonow, spec. nov.

(Figures 3 and 9D, E, F)

Material and locality: One specimen, found in coral rubble 2.5 m deep, 15 km north of Trincomalee, on 11 August 1981.

Holotype: BM(NH) 19838 W.

Description: This was a fleshy animal, 20 mm long and 10 mm wide. The crenulate mantle completely covered the foot when the animal was crawling. The body is faintly papillate, but soft and strikingly marked. The dorsum is red with faint patches of mottled yellow and red. Along the edge of the mantle is a poorly defined line of red dots, some running together, outside of which is a creamy yellow band. External to the yellow is a vivid green band edging the upper and lower surfaces (Figure 3A). The foot, also fleshy and crenulated, has similar colorings to the mantle: it is a lighter shade of red edged with yellow and green. The foot is notched and bilabiate. The head and the simple oral tentacles are green (Figure 3B).

The rhinophores are unusually close to the end of the mantle, and retract into prominent sheaths. A rhinophore bears 23 lamellae, although the last 6 do not go all the way around the organ. The stalk is very short. The color

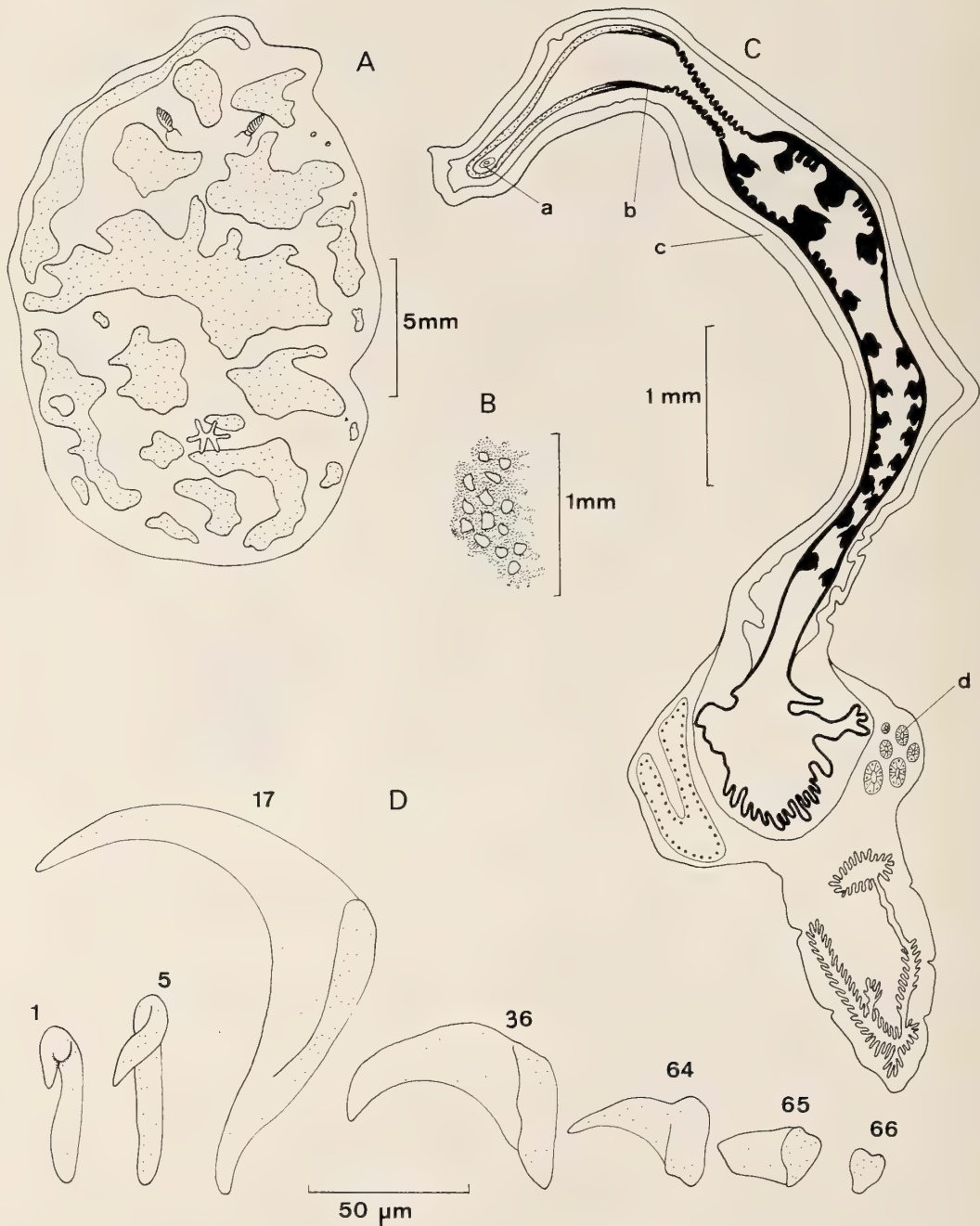


Figure 5

Platydoris scabra A. dorsal aspect of small specimen (semi-diagrammatic) drawn from preserved specimen; B. detail of dorsal pigment; C. penis (reconstruction), a = vas deferens, b = cuticularized penis, c = muscular body wall, d = accessory gland; D. radular teeth of larger specimen (with aid of camera lucida).

pattern on the rhinophore is interesting: the whole is sheathed in red, and underlying this layer is a green pigment which decreases in area towards the base, where the sides and back of the rhinophore are red and the anterior surface is green. The midline, where the lamellae stop just

short of meeting each other, is white for the entire length of the rhinophore (Figure 3C).

There are 19 fleshy gills, which retract into a large cavity with a raised edge. The outer ring consists of 11 larger gills, inside which are 8 smaller gills. They are

brightly colored, a red rachis with red pinnae at the base, green in the center, and white at the tip. When fully extended, the gills project beyond the mantle edge on both sides and at the posterior end.

The radular formula for the specimen is 38·1·38. The number of rows differs on the two sides: 109 and 116. The median tooth is triangular and the rest of the teeth vary in form and size along the row. By the third tooth, the cusp is long and, toward the new end of the radula, sharp. The knob at the juncture of the cusp and root diminishes as the teeth grow older, as does the length of the cusp. All the teeth in each row are denticulate, with 7–8 denticulations present only on one side (Figure 3D and 9D, E, F). The jaw plates are made of crescent-shaped, smoothly tapering rods, averaging 5 μ m in length.

Remarks: A number of Chromodorididae have a dorsal pattern similar to *Chromodoris adeima*, but the colors differ. *Casella atromarginata* (Cuvier, 1804) can be green with a white and black margin. *Chromodoris splendida* (Angas, 1864) is cream with red markings and a bright yellow-orange pallial edge. *Chromodoris preciosa* (Kelaart, 1859) is a white animal with a red border and yellow sub-margin. The colors of *C. adeima* as well as its radula are enough for it to be considered a distinct species.

In Greek, *adeimos* is one of the many words meaning "brave, bold and fearless."

Kentrodoris rubescens Bergh, 1876

(Figure 4)

Kentrodoris rubescens BERGH, 1876
MARCUS, 1976

Material and locality: One specimen found under a rock with much epiphytic growth 2 m deep, 15 km north of Trincomalee, on 31 July 1981.

Description: The live animal was 90 mm long and 25 mm wide. The specimen was soft, smooth, and slimy. The base color is beige with red-brown longitudinal linear markings. Yellow-green areas are present between some sets of lines. The lines are not continuous, nor of uniform thickness, so there are regions of beige devoid of lines as well as patches of red-brown where the beige is barely visible. The highest concentrations of dark pigment are found at the anterior and posterior ends, where the linear markings are shorter and thicker. The darker patches traverse the dorsum. The foot is concealed by the notum and is beige, with wavy linear markings, and the hyponotum extending beyond the foot is white. The dorsum is highest in the region of the branchiae, which are located slightly posterior to the mid-dorsum. There is a high sheath protecting a deep cavity into which a circlet of 7 gills is retracted. The gills when fully extended stand approximately 2 cm above the notum. They are bicolored: the proximal half is white and the distal red-brown. The rachis is white with branching pinnae.

The gill sheath is darker, because of converging and thickening lines, as are the prominent rhinophore sheaths. The lamellated rhinophores are almost 15 mm in length, with brown bases and white tips.

The radular formula is approximately 35 × 25·0·25. All the teeth are squared except for the last one, which is rounded. The first lateral is distinctly different from the others: the root is stronger and wider, more square than rectangular. The first 7–8 teeth of each row have a groove along the inner surface of the cusp, not present in the other teeth. The end tooth in each row differs from the others in having a very rounded end, noticeable among the squared, blunt ends. The root of this last tooth is small and not very strong (Figure 4A). The jaw plate was caustic resistant, with no recognizable substructure.

The vestibular stylet is 7.5 mm long, chitinous, and enclosed in a membrane (Figure 4B).

Platydorid scabra (Cuvier, 1804)

(Figure 5)

Doris scabra CUVIER, 1804a
Platydorid scabra: MARCUS & MARCUS, 1959
EDMUNDS, 1971
SOLIMAN, 1978

Material and locality: Two specimens found in 2–3 m, 15 km north of Trincomalee, on 11–12 August 1981.

Description: The smaller specimen was 20 mm long and 15 mm wide, the body oval and flattened. It is granular, tough, and leathery to the touch. The dorsal side of the animal is creamy yellow, almost pale orange, with brown patches and speckles. The patches are paired and nearly symmetrical: 2 small patches anterior to the rhinophores and 2 larger patches just posterior to the rhinophores, in contact with the rhinophoral sheaths. The crescent-shaped patches are larger, meeting in the center and pointing toward the gill pocket. Two patches are located anteriorly in the crescent hollows and make the pattern transversely linear again. Posterior to the branchiae are 3 small patches arranged in a semi-circle around the pocket. Around the periphery are discontinuous lighter patches. A number of small spots are scattered among the large patches and around the edge (Figure 5A). The variations in color are caused by the presence and absence of small brown dots, which converge in regions of dark color (Figure 5B).

The ventral side of the mantle is creamy, devoid of pigment. The foot, although not pigmented, is darker than the hyponotum. It does not project beyond the mantle. The sides of the foot are finely speckled with brown dots which increase in concentration to form a line in the region between the dorsal surface of the foot and the hyponotum. This line is not visible from underneath when the animal is crawling.

The pallial edge is orange, visible only in lateral view. The rhinophores are lamellated and retract into prominent sheaths 1.3 mm across. The sheaths have a smooth

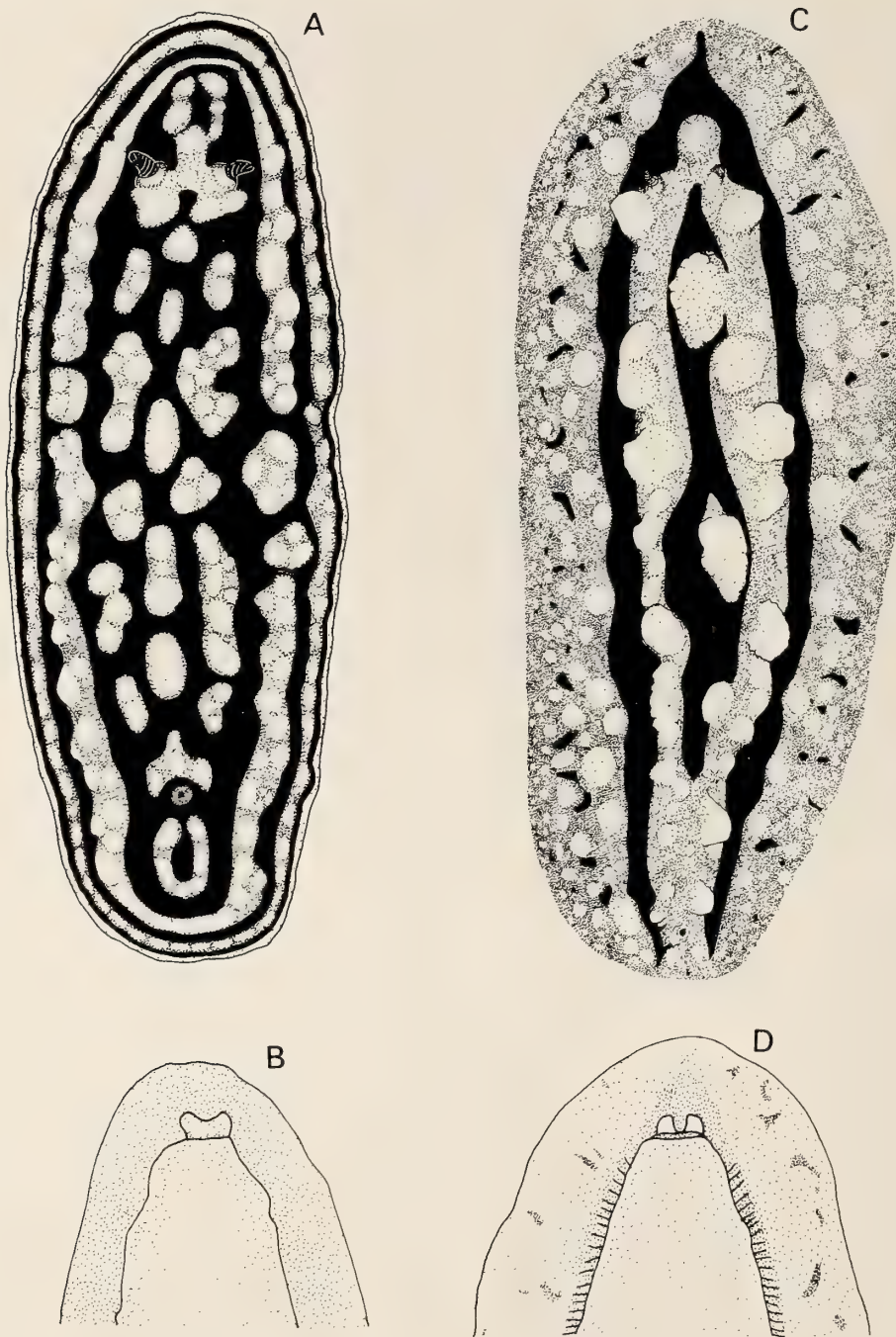


Figure 6

Phyllidia empelia Yonow, spec. nov., drawn from preserved specimen (holotype): A. dorsal aspect; B. ventral view of the head. *Phyllidia alia* Yonow, spec. nov., drawn from preserved specimen (holotype): C. dorsal aspect; D. ventral view of the head.

rim and are creamy in color, with a few faint radiating brown lines.

The 6 large gills are voluminous pinnate structures, contractile into a single cavity. The crenulated gill pocket

is star-shaped with a smooth rim, symmetrical on either side of the median. Like the rhinophoral sheaths, it exhibits the base color with even fewer markings on the outside edge; the inside is creamy.

The radular formula is $43 \times 99.0.99$, and the radula is 4.5 mm long and 3 mm wide. The teeth are long hooks, approximately 16 μm long, with relatively small roots. The first tooth, however, has a long rounded root and short cusp, but the second tooth in the first 16 rows has the typical pointed cusp. The second and subsequent teeth onwards of row 16 are twisted. The last few teeth in each row degenerate rapidly into blunt, rounded, irregular structures.

The penis was sectioned to look for spines and a reconstruction has been drawn (Figure 5C). The penis is retracted and the spines line the lumen, which is cuticularized. The spines are large boss-like structures with a small curved spine at the end, the largest measuring 450 μm high and 375 μm wide.

No description is available from life for the second specimen. In alcohol it measures 39 mm in length and is 34 mm wide. The dorsal pattern is preserved and will be described. This pattern differs from the previous specimen and from other *Platydorid* *scabra*. There is a dorsal rounded triangular shape very lightly pigmented, and the region surrounding it is dark. The brown pigment is in the form of dots identical to the smaller specimen. The pallial edges are crenulate, each indentation showing an increase of brown pigment. The area behind the gill is darkly pigmented, and the area anterior to the rhinophores is somewhat lighter. The ventral side is exactly as described for the first specimen, with a long (23 mm) narrow foot. The pigmented region between the foot and the mantle is 10 mm wide.

The rhinophore sheaths are 2 mm in diameter and the gill pocket 5 mm across.

The radular formula is $36 \times 66.0.66$. The teeth are smaller than those of the first specimen, the largest with a cusp 100.56 μm long. The teeth are as for specimen 1, the first tooth with a shorter cusp than the following teeth. The twisting-over occurs further along the row at the growing end: in row 15 the twisting is visible in the sixth tooth, but from row 19 onwards, the second tooth is twisted (Figure 5D). No recognizable substructure of the jaw plates survived caustic treatment.

Phyllidia empelia Yonow, spec. nov.

(Figures 6A, B, 7A, 8A, B)

Material and locality: Two specimens found on the sides of large rocks, 2 and 4.5 m deep, in Koduwakattumalai Bay, on 7 and 12 August 1981.

Holotype: BM(NH) 19839 W/1.

Paratype: BM(NH) 19839 W/2.

Description: The smaller specimen (holotype) is 20 mm long and 7.3 mm wide in alcohol. The oval body is elongate, completely concealing the foot. The base color is black, and the tubercles are gray. The animal is softer and more flexible than the other species of *Phyllidia* found

in Sri Lanka. The gray oral tentacles are squarish and joined together at the base. The foot is also gray, without a median line (Figure 6B).

The dorsal pattern is conveniently described from the pallial margin to the midline. A thin gray band without tubercles encircles the animal. Inside this is a thin black stripe (just visible in places on Figure 8B). Also forming a complete oval is the first row of tiny tubercles: these are gray and single, and the gray region around the bases merges into a continuous gray band. Inside this is a flat black band, followed by another row of tubercles. These are larger, 1 mm across, and multi-tuberculate, with a maximum of 3 tubercles. This row has 2 indentations in the oval, near the center at the widest point of the animal, corresponding with 3 tri-tuberculate lumps. The next black band is adjacent to and external to the rhinophores. Inside this black band the tubercles emerge with some regularity. A ring of 6 tubercles is found anterior to the rhinophores, and another ring is found posterior to the anus. The median tubercles then alternate between both sides and the center, some single and some compound. There are 9 tubercles down the center, rounded towards the anterior and posterior ends, and elongated in the middle (Figure 6A).

The rhinophores and anus are just inside the third black stripe. The black rhinophores are lamellated and large in comparison to other Phyllidiidae; the sheaths are gray. The anus is a small slightly raised gray tube exactly on the midline.

The larger specimen (paratype) is 26 mm by 10 mm in alcohol. It conforms to the above color description, but proportions vary slightly. The first gray and black lines of the margin are very fine, scarcely visible. The first row of tubercles is as described, but the tubercles in the second row are elongated transversely, forming a ring of perpendicular ridges around the edge. The four posterior tubercles merge with the outer row of single tubercles and the fine gray line that surrounds the whole. The median tubercles have the same patterns described above but there are 10 tubercles down the center (Figure 8A).

The foot is gray, lacking a median line, and is marked transversely with two black slashes; one crosses the foot and the other crosses over just half the foot. The oral tentacles are as previously described.

The long, pointed rhinophores are sheathed and lamellate. Unlike most nudibranch rhinophores, the 16 lamellae in this species are very short; they do not grow diagonally across the length of the rhinophore and they overlap each other from the base to the tip. Only at the distal tip do the lamellae actually meet in the dorsal and ventral midline of the rhinophore. The subsequent 11 lamellae stop short of the base, the last 6 running perpendicular to it. The rhinophore of this second specimen has a length of 2 mm (Figure 7B).

Remarks: This species has a number of characteristics that serve to distinguish it from other Indo-Pacific and Pacific Phyllidiidae. It seems similar to *Phyllidia nobilis*

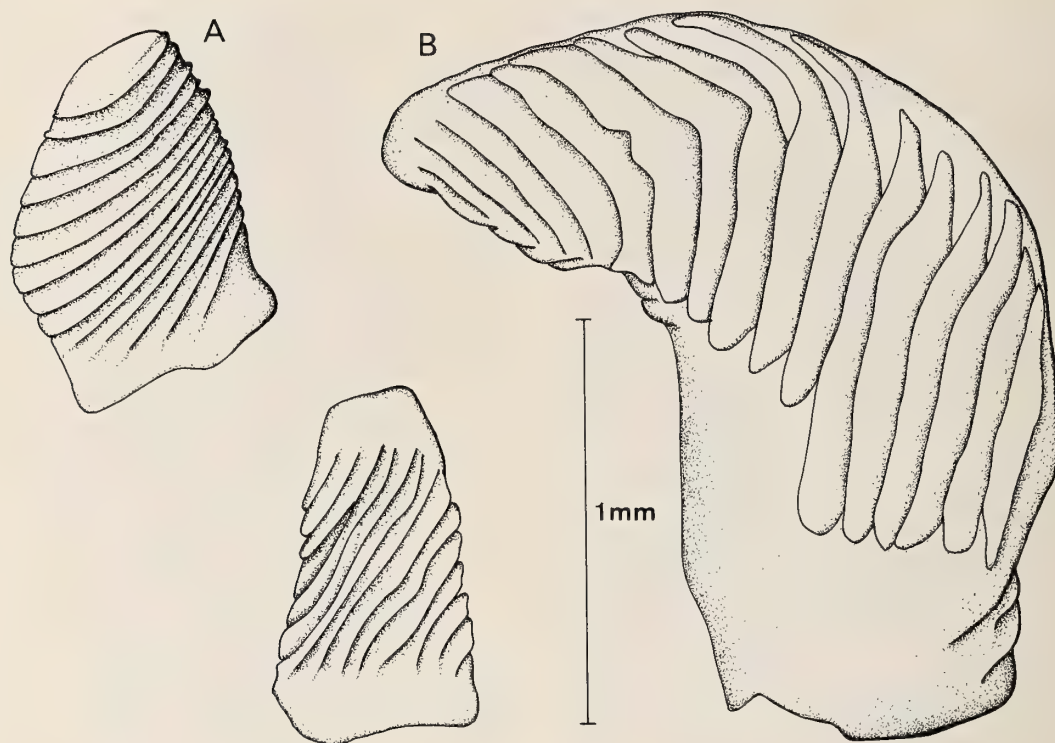


Figure 7

Rhinophores: A. *Phyllidia alia* Yonow, spec. nov., drawn from preserved specimen (holotype); B. *P. empelia* Yonow, spec. nov., drawn from preserved specimen (paratype); C. *P. varicosa*, drawn from preserved specimen.

Bergh, 1869, as described by EDMUNDS (1972), ELIOT (1904a), and RISBEC (1953). However, both Sri Lankan specimens were gray and black, with no trace of orange or green as recorded by these authors. My two specimens show some variation in size and shape of the tubercles, but follow the same sequence of pattern: two uninterrupted rows of gray tubercles surround the whole dorsum, plus one that is broken on each side but continuous around both ends. *Phyllidia albonigra* Quoy & Gaimard, 1832, from Tonga vaguely resembles *Phyllidia empelia*, but the anterior and posterior extremities of the Tongan species are pointed, and the compound tubercles are not arranged in any definite pattern. *Phyllidia zeylanica* Kelaart, 1859, is similar in pattern to *P. empelia*, but *P. zeylanica* has pink tubercles and pink and black rhinophores. On my specimens, the rhinophores are completely black, and noticeably large, a fact not mentioned by previous authors.

Because of the lack of color in this species, I have called it *empelia* from the Greek *empelios*, meaning "gray."

Phyllidia alia Yonow, spec. nov.

(Figures 6C, D, 7A, 8F, G)

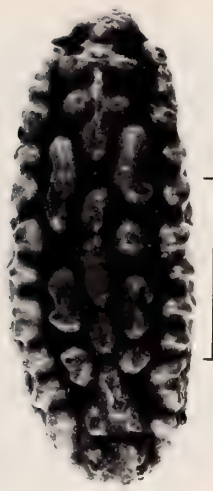
Material and locality: Two specimens found 1 m and 4 m deep, respectively, on the sides of rocks in Koduwakattumalai Bay, on 3 and 7 August 1981.

Holotype: BM(NH) 198310 W/1.

Paratype: BM(NH) 198310 W/2.

Description: The first specimen (holotype) measures 22 mm by 8.5 mm in alcohol, oval and elongate, in conformity with the majority of Phyllidiidae. In this specimen, however, the body color is white with black lines and yellow splashes on the tubercles. The white mantle edge is flattened, with tiny blisters around it, and a few spots of black. This white band is 2.5 mm wide, narrowing at the anterior and posterior ends. At its inner margin is a row of larger blisters, tipped with yellow. Two lines of black pigment run down either side, beginning at a point on the anterior edge of the mantle and ending posteriorly on either side of the anus, which is located on a yellow tubercle along the midline. These black regions are non-tuberculate. Inside this is an ellipse of large simple, grainy tubercles. The largest ones (whiter in the photograph, Figure 8F) are bright yellow in color. The smaller white tubercles have bases that tend to merge with one another. The rhinophores are located on the anterior edge of this ellipse and the anus at the posterior. The midline is a black line which divides at the base of each of 3 large yellow tubercles, running around them and meeting again on the other side (Figure 6C).

The rhinophores are bright yellow, lamellated, and



A



B



C



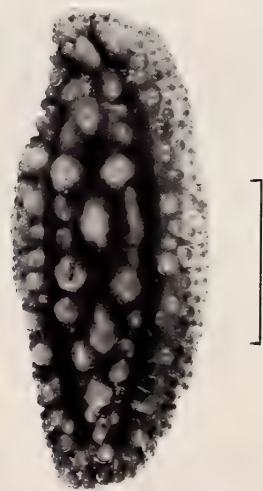
D



E



F



G

Figure 8

A and B. *P. empelia* Yonow, spec. nov.; C, D and E. *P. varicosa*; F and G. *P. alia* Yonow, spec. nov. Scale = 1 cm.

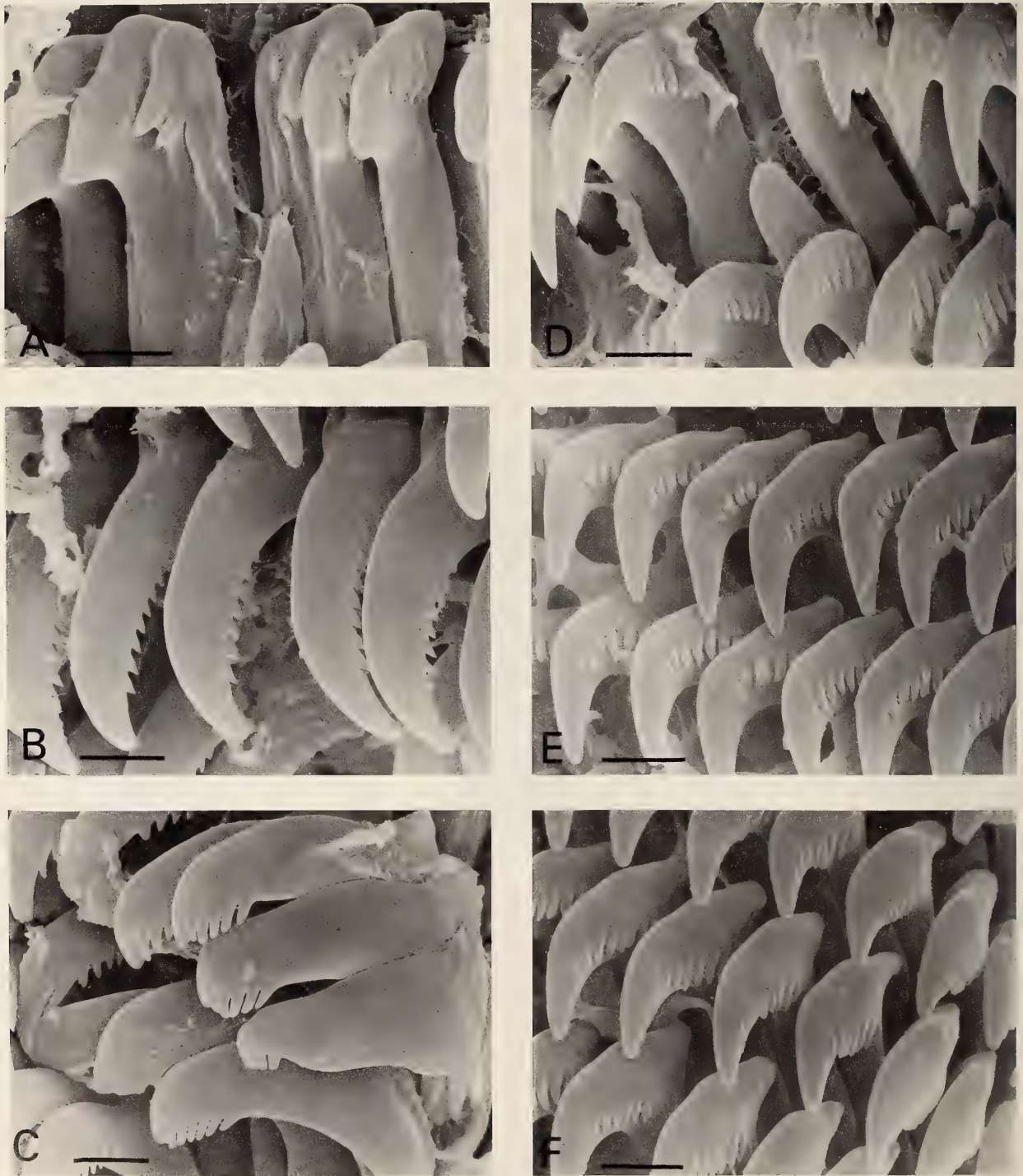


Figure 9

Scanning electron micrographs of chromodorid radulae. Scale = 10 μ m. *Chromodoris conchylata* Yonow, spec. nov.: A. midline of radula; B. center of radula; C. outer edge of radula. *Chromodoris adeima* Yonow, spec. nov.: D. midline of radula; E. center of radula; F. outer edge of radula.

sheathed. The drawing (Figure 7A) is of a preserved specimen: the rhinophores are short and squat, and the 14 lamellae run almost parallel to the sheath. They overlap each other from distal to proximal, and the last 4 do not meet at the midline. In the photographs of live material, the rhinophores are slightly curved, finger-like projections, approximately 2 mm long. The gray oral tentacles are bulbous with a rounded point on the inner edge, attached separately to the head. Surrounding the foot on the hyponotum, the gills are visible as short transverse black lines, and the dorsal pattern of black shows through the thin mantle (Figure 6D).

The second specimen (paratype) was larger, 30 mm long and 12 mm wide in alcohol. The pattern is exactly as for the first specimen, with 3 large tubercles down the central black line. The anus, located on a tubercle in the midline, can be clearly seen in the photograph (Figure 8G).

Remarks: This species was easy to establish as different from other described Phyllidiidae. The pattern is striking and almost exactly the same in both specimens. *Phyllidia alia* resembles *Phyllidia pustulosa* Cuvier, 1804, but differs in the thinness of its mantle edge, the lack of a regular pattern in the tiny blisters interspersed with black markings around the edge, and the presence of two uninterrupted black lines on the dorsum. *Phyllidia pustulosa* is said (PRUVOT-FOL, 1956) to have "tubercles on the pallial edge sometimes grouped in triangular shapes, reminding one of drawings of *Phyllidia varicosa* Lamarck, 1801, and *Phyllidia elegans* Bergh, 1869. In general, in most of the individuals figured, there are only vague irregular rows on the edge of the mantle." BABA & HAMATANI (1975) describe *P. pustulosa* as slightly variable, but generally with compound warts of 2–6 partially-united smaller warts. The tubercles around the margin tend to be isolated. CUVIER's (1804b) drawing of *P. pustulosa* does not resemble these specimens. PRUVOT-FOL (1956) has further confused matters by misspelling *P. pustulosa* as *P. pustulata* in the heading of her description. Neither she, BABA & HAMATANI, nor CUVIER refer to the two distinct black lines on the dorsal surface, which serve to distinguish *P. alia* species from any other *Phyllidia*.

Alia is Latin, meaning "another."

Phyllidia varicosa Lamarck, 1801

(Figure 7C, 8C, D, E)

Phyllidia varicosa LAMARCK, 1801

ELIOT, 1904b

EDMUNDS, 1972

BABA & HAMATANI, 1975

P. trilineata CUVIER, 1804b

QUOY & GAIMARD, 1832

Material and locality: Three specimens found at depths of 1 m and 4 m in Koduwakattumalai Bay, on 3 and 7 August 1981.

Description: The specimens are oval in shape and hard to the touch. All have the distinctive mark of *Phyllidia varicosa*: an interrupted black line down the center of the gray foot.

Specimen 1 measures 28 mm by 14 mm (22 mm × 10 mm in alcohol) and has the dorsal markings of a typical *P. varicosa*. Two pairs of black lines run longitudinally, with 3 ridges of yellow-tipped tubercles between them. The tubercles have a grainy appearance. The central ridge terminates with a knob containing the anus. The ridges on either side begin just posterior to the rhinophores. The edge of the mantle is more solid than in the other two species and contains ridges of tubercles alternating with solitary tubercles, surrounded by black. The first tubercle of each transverse ridge is large and yellow. The solitary tubercle is sometimes followed by a row of small tubercles down to the mantle edge. Some of these second tubercles are also yellow.

The yellow rhinophores are sheathed, finger-like projections with 14 lamellae running diagonally down the organ. They start in a straight line at the distal end and stop in a straight line just before the base, which makes them conspicuous. The rhinophore is almost symmetrical in lateral view, like a tall trapezoid with a narrow base (Figure 7C).

Specimen 2 measures 55 mm by 25 mm in alcohol. The markings are similar to specimen 1, but the 3 rows of tubercles down the back cannot be described as ridges: they are more like tubercles with their bases merging, less delicate than the first specimen. These tubercles are orange. The orange rhinophores are sheathed and lamellated, located as described above. The anus is present on the last median tubercle.

Specimen 3, measuring 39 mm by 16 mm in alcohol, is a more extreme form of specimen 2: the typical pattern is still present, but more indistinct. The orange tubercles are all much larger, elongated projections, different from the grainy ridges of specimen 1. The first tubercles of the transverse rows merge longitudinally, creating a discontinuous third band of tubercles. The other details are as described above.

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Technique for Narcotizing and Fixing Veliger Larvae of *Amphibola crenata*

by

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Abstract. A three-stage method for narcotizing veliger larvae is described, using calcium-free seawater followed by isotonic $MgCl_2$ and then a benzocaine-procaine mixture. Completely expanded veligers of *Amphibola* can be prepared for scanning and transmission electron microscopy and light microscopy.

INTRODUCTION

TO EXAMINE development of veliger larvae of the marine pulmonate *Amphibola crenata* (Gmelin), we wished to fix them with the velar lobes extended in the normal swimming position. Initial tests using gradual addition of alcohol and isotonic (7.5%) $MgCl_2$, and bubbling CO_2 through the seawater resulted in retraction of the velum and closure of the operculum, either during the narcotization or upon addition of fixative. Use of chlorobutanol as devised by BONAR & HADFIELD (1974) and subsequently employed by BICKELL & CHIA (1979) with nudibranch veligers was successful with newly hatched *Amphibola* larvae, but even when used at low temperature it caused older larvae to retract. The following three-stage method was developed and resulted in successful fixation for scanning electron microscopy (SEM), which required a high success rate, for transmission electron microscopy (TEM), and for 1 μm plastic sections for light microscopy (LM).

TECHNIQUE AND RESULTS

Veligers were raised from egg masses as described by PILKINGTON & PILKINGTON (1982). They were placed in seawater in a solid watch glass and viewed under a dissecting microscope. Sub-stage illumination was used, and this produced a slight warming that seemed to aid the narcotization process. The following procedure applies to larvae

in seawater, and appropriate dilutions must be made if lower concentrations are used.

Stage I: Seawater was gradually replaced by calcium-free seawater (with tonicity maintained by slightly increasing magnesium concentration) (Table 1) over a period of about 10 min, using a Pasteur pipette. The intention was to block synaptic transmission, as calcium-free salines have been shown to do this in other molluscan systems (*e.g.*, BERRY & PENTREATH, 1979). The treatment allowed the larvae to continue swimming, but appeared to block the normal retraction into the shell that is caused by chemical or tactile stimulation.

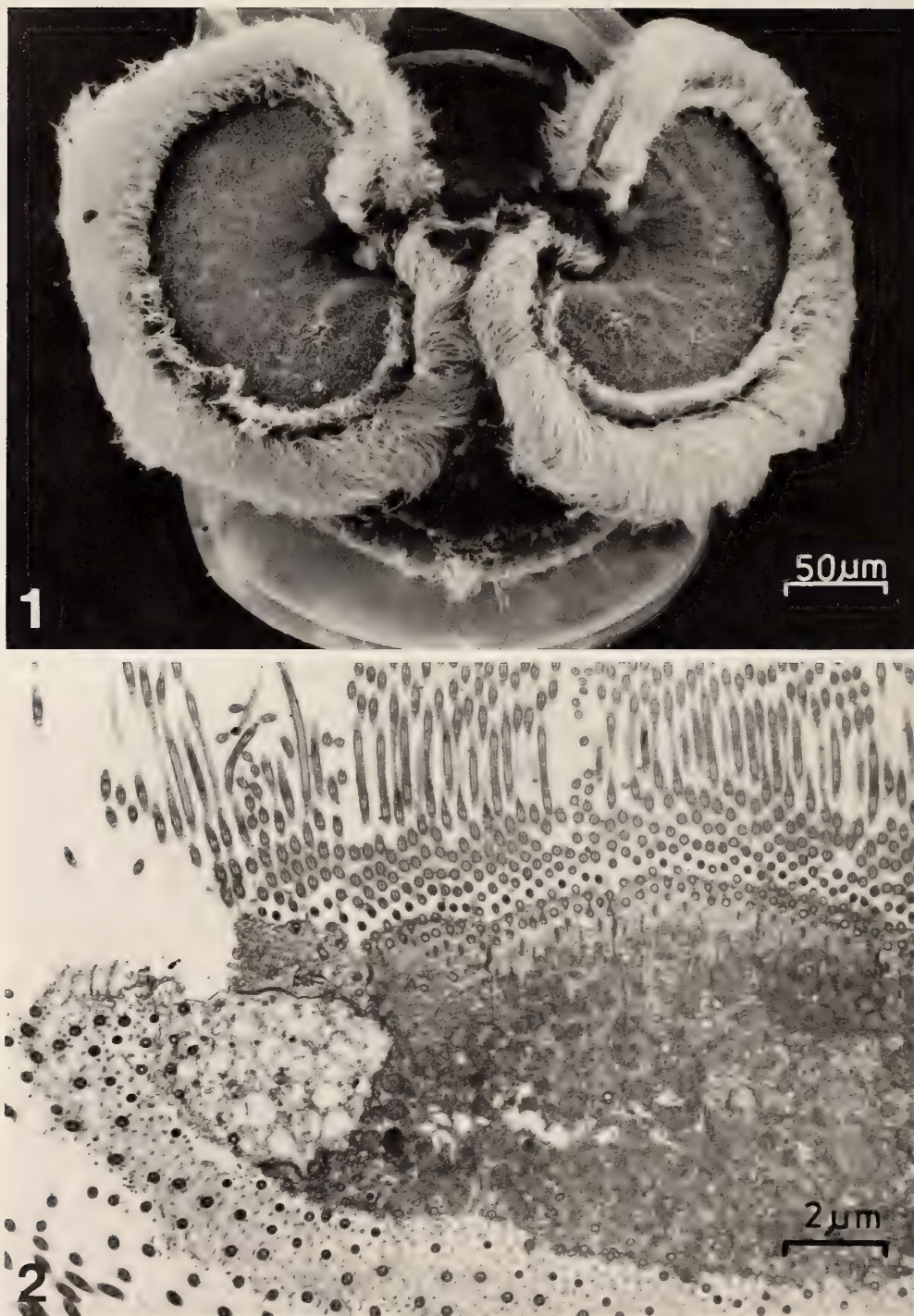
Stage II: The calcium-free seawater was gradually replaced by isotonic $MgCl_2$, and the larvae were left in this for approximately 5 min while the final narcotizing solution was prepared. Isotonic $MgCl_2$ is a well known narcotic for marine invertebrates (*e.g.*, GRIMSTONE & SKAER, 1972), but resulted in retraction into the shell if applied before Stage I. The $MgCl_2$ solution slowed the swimming rate of the larvae so that, although the cilia were still beating, the larvae gathered at the bottom of the watch glass.

Stage III: The final narcotizing solution contained benzocaine (ethyl-4-aminobenzoate) and procaine hydrochloride (Table 1). The $MgCl_2$ solution was gradually replaced with this mixture, which was added to a full watch glass to minimize turbulence. The veligers were left in it for approximately 10 min until the cilia stopped beating. Benzocaine is a widely used narcotic for fish (*e.g.*, McERLEAN & KENNEDY, 1968), but if applied without Stages I and II caused retraction.

At any stage in the procedure until the cessation of

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Explanation of Figures 1 and 2

Figure 1. Frontal SEM view of a 4-wk-old veliger with the velar lobes in the extended position. The opening of the mantle cavity can be seen dorsally between the two lobes. Below the velum is the foot and part of the operculum. Scale bar = 50 μm .

Figure 2. TEM view of the velar food groove with pre-oral cilia above and post-oral cilia below. A mass of mucous cells lies internal to the groove. Scale bar = 2 μm .

Table 1
Composition of solutions.

Calcium-free seawater (g/L distilled water)		MgCl ₂ (g/L distilled water)	Final narcotizing solution (g/5 mL ethanol)		Fixative
NaCl	33.5	MgCl ₂ ·6H ₂ O	75	Benzocaine 0.1	2.5% glutaraldehyde in 0.1 M cacodylate buffer at pH 7.6 (Should be made up fresh each day.)
MgCl ₂ ·6H ₂ O	12.3			Procaine 0.002	
Na ₂ SO ₄	3.9			Add to this 45 mL	
KCl	0.66			50% seawater	
NaHCO ₃	0.4			(Must be made up immediately before use.)	

ciliary beating, the narcotization can be reversed by replacing the fluid surrounding the larvae with seawater.

Fixation: A few drops of fixative (see Table 1) were added. The fixative reacted with the final narcotizing solution, so most of the fluid in the watch glass was removed rapidly and fresh fixative added. This procedure was repeated twice.

After fixation, veligers were rinsed several times in 0.1 M cacodylate buffer and postfixed in 1% OsO₄ in 0.1 M cacodylate buffer. The larvae were then ready for dehydration and preparation for SEM by critical point drying. For TEM and LM, veligers were embedded in resin. Thick sections (for LM) were cut with glass knives. We did not use decalcification techniques such as those described by BONAR & HADFIELD (1974), but cut thin sections (for TEM) using a diamond knife.

Results: Thirty to fifty percent of specimens were fixed successfully with the velum completely extended. The remainder had partly extended velar lobes, and very few were completely closed. The method was more successful with newly hatched veligers than with those 4–5 weeks old and about to metamorphose. Figure 1 shows a 4-wk-old veliger with the velar lobes fully extended. Figure 2 shows a TEM section of one of the velar lobes.

DISCUSSION

Although the early work of CARTER (1926) identified nicotine as a useful narcotic for the velar cilia of veliger larvae, MACKIE *et al.* (1976) found magnesium chloride more effective as a general narcotic for veligers of *Mangelia*. Our observations showed that MgCl₂ did narcotize the veligers of *Amphibola*, but under this narcosis they were still capable of retracting into the shell upon addition of fixative. The procedure described here prevented this reaction.

Although SEM has been a useful tool in describing the shells of larval gastropods (*e.g.*, ROBERTSON, 1972; THIRIOT-QUIÉVREUX & SCHELTEMA, 1982), and has been used to examine bivalve larvae (*e.g.*, LUTZ *et al.*, 1982), we have been able to find only one previous use of SEM showing veligers with expanded velar lobes (CHIA & KOSS, 1978). Even in this case, the velum was not completely

expanded into the swimming position. We have not yet been able to test the technique described here on other veligers, but if our three-stage approach can be applied to a wide range of gastropod larvae, it should allow wider use of electron microscopy to describe both their external surface and their internal structure.

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New Species of Northeast Pacific Archaeogastropods

by

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Abstract. Eight new archaeogastropods from the northeastern Pacific are described: *Anatoma baxteri*, *Puncturella rothi*, *Margarites hickmanae*, *Calliostoma titanium*, *C. bernardi*, *Lirularia discors*, *Halistylus genecoani*, and *Homalopoma draperi*.

THE NEW SPECIES described here are to be included in a report on the rhipidoglossate archaeogastropods of the northeastern Pacific from Alaska to Baja California (McLean, in preparation). Generic and subgeneric allocations are discussed in that work, which also includes new subfamilial classifications.

Abbreviations for the museum collections mentioned in the text are: AHF, Allan Hancock Foundation (collection at LACM); CAS, California Academy of Sciences, San Francisco; LACM, Los Angeles County Museum of Natural History; NMC, National Museum of Canada, Ottawa; USNM, National Museum of Natural History, Washington.

Family SCISSURELLIDAE

Anatoma Woodward, 1859

Anatoma baxteri McLean, spec. nov.

(Figure 1)

"*Scissurella* (*Anatoma*) *lamellata* (A. Adams, 1862)," McLEAN, 1967:406. Not *Anatomus lamellatus* A. Adams, 1862.

Description: Shell small for genus, low-spired, fragile, translucent grayish white. Protoconch diameter 0.2 mm; teleoconch whorls $2\frac{1}{4}$; first teleoconch whorl smooth, rounded; suture deeply impressed in first quarter whorl; fine axial ribs appear in second quarter, selenizone appearing in fourth quarter of first whorl. Selenizone at periphery, slit open $\frac{1}{5}$ of circumference, bordered by sharp raised edges. Axial sculpture of sharp, thin ridges, curved protractively near suture on upper half of whorl, retractively curved across base. Spiral sculpture of fine striae throughout, much weaker than axial ribs and not crossing them. Peritreme complete at all growth stages; umbilicus partially obscured by reflection of inner lip. Suture laid

below lower bordering ridge of selenizone, forming deep channel of same width as selenizone; suture descending slightly on last quarter of final whorl, increasing width of subsutural channel to twice that of selenizone.

Dimensions: Height 1.8 mm, diameter 2.3 mm (holotype).

Type material: 30 specimens from the type locality (many in poor condition), dredged by Rae Baxter and James H. McLean, 2 August 1973. Holotype LACM 1991, 25 paratypes LACM 1992, 2 paratypes CAS 033360, 2 paratypes USNM 784743.

Type locality: 9 m off N side Hesketh Island, Kachemak Bay, Kenai Peninsula, Cook Inlet, Alaska (59°30.5'N; 151°31.0'W).

Referred material: 5 lots in the LACM collection, from the type locality east to Torch Bay, Glacier Bay National Monument, Alaska, in depths of 10-45 m on gravel and mud bottoms. Specimens from Torch Bay were collected by Tom Suchanek.

Comparisons: I previously (McLEAN, 1967) identified this species as *Scissurella* (*Anatoma*) *lamellata* (A. Adams, 1862), which occurs at 50-700 m in central Japan (KURODA *et al.*, 1971; other references in McLEAN, 1967). This species differs from the latter in its smaller size (maximum diameter of 2.3 mm rather than 3.5 mm), and lenticular rather than high-turbinate profile. It is the only eastern Pacific species of *Anatoma* having the axial sculpture much stronger than the spiral sculpture.

Remarks: I follow POWELL (1979) in regarding the differences between *Scissurella* Orbigny, 1824, and *Anatoma* at the generic rather than subgeneric level.

Named after Rae Baxter, Alaska Department of Fish and Game, Bethel, Alaska, who has collected this species from many localities in Alaska.



Figure 1

Anatoma baxteri McLean, spec. nov. Three views of holotype; height 1.8 mm.

Family FISSURELLIDAE

Puncturella Lowe, 1827

Puncturella rothi McLean, spec. nov.

(Figure 2)

Description: Shell of moderate size for genus, relatively thin; basal outline elongate oval, narrower anteriorly; sides distinctly compressed, nearly parallel. Anterior slope slightly convex, posterior slope slightly concave, lateral slopes nearly straight. Apex approximately central, eroded to blunt, posteriorly directed spur. Foramen long and narrow, constricted in middle, anterior portion narrowed and tapering. Radial sculpture of approximately 30 strong primary ribs originating near apex, secondary ribs emerging when shell is half-grown; secondary ribs not quite attaining same size as primary ribs, but filling interspaces; ribs finely and sharply beaded corresponding to growth increments. Exterior pattern of radial sculpture visible in shell interior; muscle scar not apparent; margin finely crenulated by primary ribs. Septum broadly arched, slanted forward, anteriormost extension of septum continuous with wedge-shaped callus that borders foramen, terminating 3 mm from anterior margin; base of septum with weak lateral extensions or props.

Dimensions: Length 15.0 mm, width 10.5 mm, height 8.0 mm (holotype).

Type material: 4 specimens (1 with remains of mantle tissue, indicating that it was live-collected) from the type locality, collected by the R/V "N. B. Scofield," station B.8, 6 October 1950. Holotype CAS 033361, paratype CAS 033362, paratype LACM 1993, paratype USNM 784744.

Type locality: 521–283 m (285–155 fm), Delgada Canyon, off Buck Creek (approximately 40°05'N; 124°08'W), Humboldt County, California.

Comparisons: *Puncturella rothi* differs from *P. galeata* (Gould, 1846) in its smaller size, more parallel sides, stronger development of beaded sculpture, larger septum, larger foramen, and absence of sharp ridges that form props to the septum.

Remarks: *Puncturella rothi* is known only from the type lot. It has the general appearance of *Cranopsis decorata* (Cowan & McLean, 1968), but does not have the anterior seam in the shell nor the split mantle roof that distinguishes *Cranopsis* A. Adams, 1860. All specimens have the apical area eroded. This species occurs at depths greater than those of other eastern Pacific species of *Puncturella*; it lives at depths characteristic for *Cranopsis decorata*.

Named after Dr. Barry Roth of the California Academy of Sciences, San Francisco.

Family TROCHIDAE

Margarites Gray, 1847

Margarites hickmanae McLean, spec. nov.

(Figures 3, 9)

"*Margarites beringensis* E. A. Smith," DALL, 1925:19, pl. 36, figs. 4, 6. Not *Valvatella beringensis* E. A. Smith, 1889.

Description: Shell moderately large for genus, cream-colored under thin, pale brown, shiny periostracum. Protoconch smooth, tip pointed, protoconch diameter 0.35 mm; teleoconch whorls 5; early suture slightly impressed, becoming deeper on later whorls; suture gradually descending on final whorl. Last whorl broadly inflated; aperture markedly oblique, umbilicus narrow. Peritreme nearly complete; inner lip thick, parietal lip reflected, almost blocking umbilicus. Spiral sculpture of fine, microscopic incised lines, about 24 on penultimate whorl, 18 on body whorl; axial sculpture of fine growth lines. Interior iridescent, chiefly lavender. Lateral teeth of radula 7 pairs, overhanging tips long and tapered, tips rounded, both edges finely denticulate.

Dimensions: Height 10.1 mm, diameter 12.2 mm (holotype).

Type material: 14 specimens (all but one specimen live-collected and dried with opercula in place) from the type locality, dredged by the U.S. Fisheries Commission R/V "Albatross," station 4779, 5 June 1906. Holotype, USNM 111048, 9 paratypes USNM 205827, 2 paratypes LACM 1994, 2 paratypes CAS 033363.

Type locality: 99 m (54 fm) on sand and shell bottom, Petrel Bank (near Semisopochnoi Island, Rat Islands, Aleutian Islands), Bering Sea, Alaska (52°11'N; 179°57'W).



Explanation of Figures 2 to 8

Figure 2. *Puncturella rothi* McLean, spec. nov. Three views of holotype; length 15.0 mm.

Figure 3. *Margarites hickmanae* McLean, spec. nov. Two views of holotype; height 10.1 mm.

Figure 4. *Calliostoma titanium* McLean, spec. nov. Holotype; height 32.2 mm.

Figure 5. *Calliostoma bernardi* McLean, spec. nov. Holotype; height 25.7 mm.

Figure 6. *Calliostoma bernardi* McLean, spec. nov. Paratype; height 26.5 mm.

Figure 7. *Lirularia discors* McLean, spec. nov. Two views of holotype; height 4.3 mm.

Figure 8. *Homalopoma draperi* McLean, spec. nov. Three views of holotype; height 4.0 mm.

Referred material: Known only from the type lot.

Comparisons: This is the only member of *Margarites*, s.s., in which there are 7 pairs of lateral teeth in the radula (Figure 9). Such similarly proportioned, shallower occurring species as *M. helacinus* (Phipps, 1774), *M. beringensis*

(E. A. Smith, 1899), and *M. albolineatus* (E. A. Smith, 1899) lack spiral sculpture and have 6 pairs of lateral teeth in which the tips of the outer laterals are broader than those of *M. hickmanae*. In size the new species most resembles the offshore *M. gigantea* (Leche, 1878), but that species has 4 pairs of lateral teeth, a less inflated final



Figure 9

Margarites hickmanae McLean, spec. nov. Half row of radula of holotype, showing rachidian at left, 7 marginal teeth, latero-marginal plate, and first 2 marginal teeth.

whorl, and a darker, dull-surfaced periostracum. *Margarites hickmanae* is larger than *M. argentata* (Gould, 1841), which has 5 pairs of lateral teeth. (*M. pribiloffensis* Dall, 1919, is here regarded as a synonym of *M. argentata*, the holotype having 5 pairs of laterals.)

Remarks: The holotype of *M. hickmanae* was figured by DALL (1925) under the name *M. beringensis* (E. A. Smith, 1899), a species described from the Commander Islands (west of the westernmost of the Aleutian Islands). *Margarites beringensis* differs in having a glossy brown surface and gray early whorls; it is common at low tide in Alaska and British Columbia.

The name honors Dr. Carole S. Hickman of the Department of Paleontology, University of California, Berkeley.

Calliostoma Swainson, 1840

Calliostoma titanium McLean, spec. nov.

(Figure 4)

Description: Shell large for genus, sturdy, white, protoconch diameter (of smallest specimen) 0.4 mm, teleoconch whorls 7. Whorls only slightly rounded, shoulder slightly tabulate; base defined by moderately sharp keel. First 3 teleoconch whorls with strong, unbeaded spiral cords; spiral sculpture of subsequent whorls very subdued except for subsutural cord; subsutural cord prominently beaded on fifth whorl; fine, even spiral cords emerge on fifth whorl; 16 spiral cords on penultimate whorl; all cords microscopically beaded on final whorl. Suture laid upon basal angulation; base imperforate, smooth, with fine spiral striae, more strongly developed near columella. Aperture quadrate, outer lip thin, columella thick, slightly reflected. Interior iridescent pink and green.

Dimensions: Height 32.2 mm, diameter 30.0 mm (holotype); height 27.4 mm, diameter 25.3 mm (paratype).

Type material: 2 specimens from the type locality dredged by the R/V "Velero," station 1027-39, 10 December 1939. Holotype LACM 1995, paratype USNM 784745.

Type locality: 256–274 m (140–150 fm) on green mud, 8.3 km (5 miles) SE of Santa Catalina Island, California (33°15'N; 118°14'W).

Referred material: Two additional specimens: one (LACM-AHF 1151-40), 214–234 m (117–128 fm) near type locality (33°16'N; 118°16'W), collected 5 July 1940, height 29.5 mm, diameter 28.4 mm; and one (LACM 92119), from 300 m, "Cortes Bank," California, collected August, 1968, by Shane Anderson, height 18.8 mm, diameter 17.7 mm.

Comparisons: Although *Calliostoma titanium* has its third and fourth whorls without spiral sculpture, as in *C. platinum* Dall, 1890, it differs from the latter in having a sturdier shell, a subsutural tabulation, and numerous fine cords on the final whorl. It is larger than *C. bernardi* McLean, spec. nov., from which it also differs in having the third and fourth whorls smooth rather than having strong spiral cords on all whorls; the cords on the body whorl are more numerous and finer than those of *C. bernardi*.

Remarks: This and the following new species have been known to me for many years, not having been described until now in the futile hope of obtaining more material.

The name is that of a metallic element, emphasizing lack of shell color, and contrasting with *C. platinum*.

Calliostoma bernardi McLean, spec. nov.

(Figures 5, 6)

Description: Shell medium-sized for genus, sturdy, white; protoconch diameter 0.4 mm, teleoconch whorls 7½. Early whorls flat-sided except for strongly projecting subsutural cord; final whorl rounded, losing sharp basal angularity of previous whorl. First 3 teleoconch whorls with 3 strong, unbeaded spiral cords, intercalary cords of lesser strength appearing on fourth whorl; original cords becoming beaded on fourth whorl; penultimate whorl with 9 somewhat irregular cords, uppermost of these beaded; body whorl with about 13 cords above ill-defined periphery, uppermost of these finely beaded. Base imperforate, mostly smooth but for fine spiral striae, basal cords more strongly developed toward columella. Aperture rounded, outer lip thin, columella thick. Interior iridescent pink and green.

Dimensions: Height 25.7 mm, diameter 22.8 mm (holotype); height 26.5 mm, diameter 22.8 mm (paratype).

Type material: Holotype LACM 1996; single specimen only from type locality, collected by the R/V "Velero," AHF station 1152-40, 5 July 1940. One paratype, NMC 86653, 128 m (70 fm), Halibut Bank, Georgia Strait, British Columbia (49°18'42"N; 123°41'06"W), collected by Frank R. Bernard, 11 October 1968.

Type locality: 241–271 m (132–148 fm), off SE end of Santa Catalina Island, California (33°15'40"N, 118°13'25"W).

Comparisons: *Calliostoma bernardi* is closest to *C. titanium* McLean, spec. nov., but is smaller and has pronounced spiral sculpture at all growth stages, rather than having the nearly smooth third and fourth whorls of both *C. titanium* and *C. platinum* Dall, 1890.

Remarks: Although only two specimens from well separated localities are known, the fact that they are conspecific argues against the possibility that this is a variant of *C. titanium*, which would be a major concern if only the southern specimen were known. I prefer not to designate paratypes from other than the type locality, but make an exception in this case.

Named after Dr. Frank R. Bernard, of the Fisheries Research Board of Canada, Nanaimo, British Columbia, who submitted the paratype specimen.

Lirularia Dall, 1909

Lirularia discors McLean, spec. nov.

(Figure 7)

"*Lirularia succincta* (Carpenter)," McLEAN, 1969:21, fig. 8-3. Not *Gibbula succincta* Carpenter, 1864.

Description: Shell medium-sized for genus; color variegated dark brown and cream, cord interspaces with yellowish green metallic luster, particularly on base. Periostracum extremely thin, barely detectable. Protoconch dark brown, diameter 0.2 mm; teleoconch whorls 4½, suture distinct but not deeply impressed; aperture oblique, umbilicus deep, narrow; peritreme interrupted in parietal area, inner lip moderately thick, not reflected over umbilicus. Spiral sculpture of strong cords: rounded mid-whorl carination on first teleoconch whorl, two cords of lesser prominence added on second whorl; penultimate whorl with three major cords and start of lesser, intercalary cords; cords on body whorl alternating in strength. Suture descending on final whorl to expose fourth major cord defining base. Axial sculpture lacking except for fine growth lines. Basal cords usually 7: two outermost cords strong, two middle cords narrower, and three near umbilicus strong and broad; this produces a shallow channel midway between basal angularity and umbilicus, producing also a slight indentation in basal lip. Umbilical wall smooth. Interior iridescent pink and green.

Dimensions: Height 4.3 mm, diameter 4.3 mm (holotype).

Type material: 60 specimens from the type locality, collected by James H. McLean, 12 August 1963. Holotype LACM 1997, 49 paratypes LACM 1998, 5 paratypes CAS 033364, 5 paratypes USNM 784746.

Type locality: 4–7 m on rocky bottom, south side of Pun-

ta Banda (near the blowhole), Baja California Norte, Mexico (31°43.6'N; 116°43.0'W).

Referred material: 62 additional lots are in the LACM collection, from numerous localities between Pacific Grove, California, and Isla Cedros, Baja California. The species is common in rocky intertidal and sublittoral zones to 20 m, particularly in areas with cool upwelling.

Comparisons: This differs from *L. succincta* (Carpenter, 1864) in having stronger spiral cords, a more angulate base, and a color pattern of variegated brown and white, rather than uniform gray. Both species have the same kind of broad channel on the base, a feature shared by no other member of the genus. *Lirularia optabilis* (Carpenter, 1864) is a much larger species restricted to and common in the Pleistocene of southern California. *Lirularia acuticostata* (Carpenter, 1864) differs in having regular, sharp axial lamellae.

Remarks: *Lirularia succincta*, the species most closely related to *L. discors*, occurs from Cook Inlet, Alaska, to Piedras Blancas Point, San Luis Obispo County, California. Both species are sympatric in central California between the Farallon Islands and San Luis Obispo County. Here the habitat is partitioned: *L. succincta* is abundant in the intertidal zone and *L. discors* occurs in the shallow sublittoral zone, as shallow as 2 m. South of the range of *L. succincta*, *L. discors* is sublittoral, and, in areas of cool upwelling (as at the type locality), it is also intertidal.

The name is a Latin adjective, meaning "different."

Halistylus Dall, 1890

Halistylus genecoami McLean, spec. nov.

(Figure 10)

Description: Shell small (normal for genus), sturdy, high-spired; nacreous interior lacking. Protoconch diameter 0.2 mm; teleoconch whorls 7, first 3 whorls low spired, dome-shaped in profile; 4 final whorls turritelliform, evenly expanding, the periphery either bulging or somewhat angulate at lower ⅓ of whorl, profile nearly straight on upper ⅔ of whorl. First teleoconch whorl smooth, rounded, suture not deeply impressed. Second whorl with 5 strong, broad, low, spiral cords; first, third, and fifth cords more prominent, interspaces deeply channeled; third and succeeding whorls with addition of narrow cords in interspaces between major cords. Mature sculpture of 4 broad, rounded cords spaced across lower ⅔ of whorl, interspaces about twice breadth of major cords and filled by about 3 fine cords between each large cord; upper third of whorl with about 4–6 fine cords of varying strength. Subsutural cord strong, sharply defining the incised suture. Base with about 7 strong, flat-topped cords; interspaces of equal width, having 1–3 narrow, sharp cords, separated by deep incisions. Aperture circular, peritreme of juvenile shell incomplete, lip of young shells sharp, crenulated by spiral



Explanation of Figures 10 and 11

Figure 10. *Halistylus genecoani* McLean, spec. nov. Holotype; height 5.6 mm.

Figure 11. *Halistylus pupoideus* (Carpenter). LACM 75-96, 18 m off Torrance Beach, Los Angeles County, California; height 4.7 mm.

cords; columellar lip raised over an umbilical chink. Mature lip beveled, thickened within; aperture slightly oblique, peritreme complete; parietal and columellar lip sharp and slightly raised; suture descending at final stage, outer lip greatly thickened below suture. Color white, yellow or tan, with irregular dark flammules. Operculum typical for genus: circular, multispiral, early volutions indistinct; 5 volutions showing on outer $\frac{2}{3}$ of radius, each volution with projecting edge.

Dimensions: Height 5.6 mm, diameter at aperture 4.4 mm (holotype).

Type material: 37 specimens (2 with opercula) collected by diving at type locality by Camm Swift and Richard W. Huddleston, R/V "Searcher" station 281, 24 October 1971. Holotype LACM 1999, 30 paratypes LACM 2000, 3 paratypes CAS 033365, 3 paratypes USNM 784747.

Type locality: 20–24 m, sandy bottom outside of kelp beds, cove at S side of Punta San Pablo, outer coast of Baja California Sur, Mexico (27°12'55"N; 114°27'30"W).

Referred material: 6 additional lots in the LACM collection, from depths of 13–55 m; 4 lots from the vicinity of the type locality in central Baja California (near Bahía San Cristobal, Isla Natividad, Bahía Tortuga, and Thurlow Head), and 2 lots from southern Baja California (Bahía Santa Maria and Arroyo Conejo).

Comparisons: *Halistylus genecoani* differs from *H. pupoideus* (Carpenter, 1864) (Figure 11) in having a carinate rather than rounded profile, spiral cords of different strength and spacing, and a less deeply impressed suture

in the first two whorls. The two species have both broad and narrow spiral cords, but the broad cords of *H. genecoani* are fewer and broader than those of *H. pupoideus*. The depth of the suture in the early whorls provides the best distinguishing character, that of *H. pupoideus* being more deeply impressed than that of *H. genecoani*.

Remarks: Both *Halistylus pupoideus* and *H. genecoani* exhibit considerable variation in strength and spacing of the spiral cords, both species having extreme forms that approach the sculpture of the other. Some specimens of *H. pupoideus* have major cords more prominent than normal, and some of the paratypes of *H. genecoani* have more rounded whorls than those of the holotype. In both species the infraspecific range of variation is greater than the interspecific difference separating extreme forms of the two species. Distributions of the two species are sympatric at 27°N latitude; however, there are too few records from the region of overlap to establish whether there are habitat differences between the two species.

The species is named after Dr. Eugene Coan, Research Associate of the Los Angeles County Museum of Natural History.

Family TURBINIDAE

Homalopoma Carpenter, 1864

Homalopoma draperi McLean, spec. nov.

(Figure 8)

Description: Shell medium-sized for genus, relatively low-spired; whorls 3, rounded; periphery rounded, suture deeply impressed, descending on final half whorl. Color pink, usually white in area of umbilical chink; some specimens with white flecks on spiral cords and predominantly white base. Protoconch diameter 0.2 mm; early whorls rounded, suture deeply impressed; early cords about 8–9, broad, even, low, with narrow interspaces; interspaces of later whorls broader than cords and with 2–3 fine cords or striae. Mature cords of irregular strength and spacing; cords on shoulder often slightly undulating. Periphery rounded, basal sculpture variable; basal cords up to 10, weaker than cords of upper part of whorl; some specimens with 2–3 broadly spaced stronger cords on base, others with more regular basal cording. Half-grown specimens narrowly umbilicate; umbilicus nearly blocked by parietal callus. Aperture of mature specimens markedly oblique; parietal callus broad, covering umbilical chink and forming projecting inner lip; callus extending in advance of aperture on base, forming distinct glazed area. Columella with one prominent tubercle. Operculum typical for genus, opaque white, externally showing 2–3 volutions, thickened on side toward columella.

Dimensions: Height 4.0 mm, diameter 4.8 mm (holotype); height 5.3 mm, diameter 5.8 mm (largest paratype).

Type material: 175 specimens (5 live-collected), collected

by diving at the type locality by James H. McLean, June and July 1971. Holotype LACM 2001, 164 paratypes (2 live-collected) LACM 2002, 5 paratypes (1 live-collected) CAS 033366, 5 paratypes (1 live-collected) USNM 784748.

Type locality: 20–30 m on gravel bottom below the boulder and kelp zone, Isthmus Cove, Santa Catalina Island, California (33°26.5'N; 118°29'W).

Referred material: 42 additional lots are in the LACM collection, mostly from depths of 20–100 m (some dead specimens from greater depths) in the vicinity of all the southern California Channel Islands (except San Miguel and Santa Barbara Islands). It replaces *Homalopoma luridum* (Dall, 1885) on gravel bottoms deeper than the under-kelp habitat favored by the latter at the Channel Islands. The southern record is Cortes Bank, California, 68 m (LACM-AHF 1335-41). North of the Channel Islands, *H. draperi* is known from a single station, 35 m off Pacific Grove, Monterey Bay (LACM 66-56). It is well represented in lower Pleistocene faunules from many offshore facies in southern California, including the Bath-House Cliff locality of the Santa Barbara Formation.

Comparisons: *Homalopoma draperi* is characterized by its low spire, numerous subdued early cords, mature sculpture that includes some cords more prominent than others on the body whorl and base, and the callus deposited on the base in advance of the aperture. *Homalopoma grippi* (Dall, 1911) is higher-spined; the latter species also has subdued basal cords, but differs in having fewer, more projecting cords on the early whorls. *Homalopoma luridum* differs in always having prominent cords of the same strength on the spire whorls and base. There is also some resemblance to *H. paucicostatum* (Dall, 1871) in the relatively few major cords on mature whorls, but that species has fewer early cords.

Remarks: This species is by far the most variable eastern Pacific *Homalopoma*. Although none has been illustrated previously, it has long been a source of confusion in collections. Some specimens are nearly devoid of sculpture, and some have rather uniform cords. These variants may be recognized as *H. draperi* in having cords on the base finer than those of the upper part of the whorl and in having a glazed basal callus.

Named after Bertram C. Draper of Los Angeles, whose photographs have illustrated many papers on eastern Pacific mollusks.

ACKNOWLEDGMENTS

I am grateful to the following collectors for the donation of type or referred material of the new species: Shane Anderson, Rae Baxter, Frank R. Bernard, Richard W. Huddleston, Tom Suchanek, and Camm Swift. Loans of type material were arranged by Barry Roth (CAS) and Joseph Rosewater (USNM). The photographs for the new species of *Anatoma* were taken by Bertram C. Draper of Los Angeles. Assistance in the preparation of other figures was provided by the LACM photography lab. I thank Eugene Coan, Myra Keen, and Patrick I. LaFollette for reading the manuscript and offering helpful suggestions.

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NOTES, INFORMATION & NEWS

In Memory of S. Ralph Hall

The members of the Long Beach Shell Club have made a generous donation in memory of their long-time member, S. Ralph Hall, who gave so generously of his time and knowledge.

The California Malacozoological Society acknowledges this donation with gratitude, and extends its sympathy to Mrs. Hall.

Important News

At its regular Annual Business Meeting on October 5, 1983, the Executive Board of the California Malacozoological Society, Inc. decided not to change the subscription rate for institutions or affiliate members. The rates for Volume 27 (July 1 to April 1) will remain at \$18.75 plus mailing charges for affiliate members of the Society and \$37.50 plus mailing charges for institutional and non-member subscriptions.

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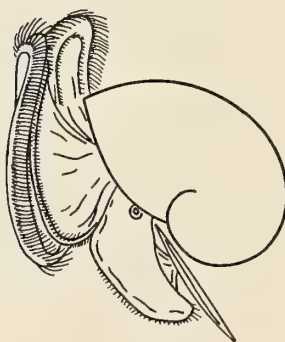
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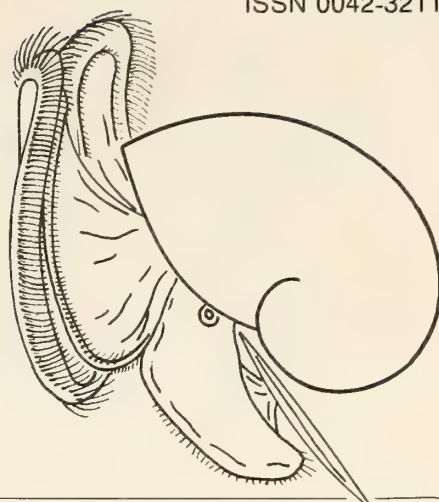
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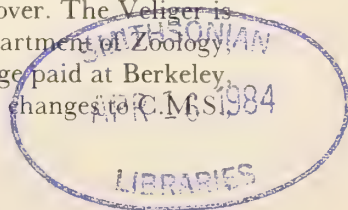
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Supplementary Information on the Morphology of *Phestilla melanobranchia* Bergh, 1874, from Seto, Kii, Middle Japan (Nudibranchia: Aeolidacea: Tergipedidae)

by

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Abstract. Four orange specimens of *Phestilla melanobranchia* Bergh, 1874, collected from the sea of Seto, Kii, Middle Japan, were kept alive in the laboratory, and the consistency of their orange pigmentation was observed. The external body form with simple branchial rows on the back margins was determined from fresh material. A histological examination of the branchial papillae was also made. In the main features of the jaws and radular teeth, the Japanese orange-colored specimens agreed well with the black-colored type-specimens of *Phestilla melanobranchia* from the Philippines to which the former was referred. Comprehensive anatomical information on the copulatory part of the genitalia is given for *Phestilla melanobranchia* for the first time.

INTRODUCTION

RECENTLY THERE appeared three successive papers by RUDMAN (1981, 1982a, b) concerning the genus *Phestilla* from Tanzania, Queensland (Australia), and the Bay of Panama (Mexico). Previous to him, the highly modified life of *Phestilla* in association with prey corals had been the subject of studies by KAWAGUTI (1943) and HARRIS (1968) on the basis of specimens obtained by them from several stations in the central Pacific and southwest Pacific, including Japan. Fortunately I was able to contact each of them in order to identify the specimens of *Phestilla* they studied.

Phestilla sibogae Bergh, 1905, which appeared in KAWAGUTI (1943), was based on a specimen (25 mm long when alive, and 10 mm long when preserved) collected on *Porites* from Palau, 29 March 1940 (Figure 1). According to RUDMAN (1981) this name was preoccupied by *Cratenia? lugubris* Bergh, 1870, which also had priority over *Aeolidia edmondsoni* Ostergaard, 1955. The species *Phestilla lugubris* (Bergh, 1870) was thus revealed to be distributed over a wide range between the Indian Ocean, southwest Pacific, and central Pacific. Up to now this species has appeared to be well studied anatomically and ecologically by different authors.

Phestilla melanobranchia, which formed the subject of work by HARRIS (1968), was established by BERGH (1874) on the basis of preserved specimens from the Philippines. Apparently the species was so named because of the possession of black (schwarzgrau oder schwarz) papillae on the back margins. However, HARRIS (1968) noted that the

papillae of *Phestilla melanobranchia* in his collection varied between orange and black depending on the specimen.

The purpose of this paper is to describe live specimens of orange-colored *Phestilla* from Japan, their identification being assured by a series of features that were originally known from the black type-specimens of *Phestilla melanobranchia*. Moreover, it is hoped that this paper will offer more extensive morphological information on this species.

TAXONOMY OF MATERIALS

Phestilla melanobranchia Bergh, 1874
(orange color form)

(Japanese name: Iboyagi-mino-umiushi)

(Figures 2 to 5)

Main synonymy:

Phestilla melanobranchia. HARRIS, 1968:193–198, figs. 1–2; Hawaii; Seto, Kii; Okinawa; Zamboanga (Philippines); Singapore; on *Tubastraea*.

Refer also to: EDMONDSON (1946), KAY (1979), GOSLINER (1980), BERTSCH & JOHNSON (1981), and RUDMAN (1981).

Main material examined: Four specimens collected from Seto, Kii, Middle Japan, 1–4 m deep, L. Harris collector, 19 September 1967. These were found on orange colonies of *Tubastraea aurea* (see HARRIS, 1968:196).

Specimen No. 1. Bright orange individual; length 20 mm.
Kept alive for about 50 days; at first fed with *Tubastraea*

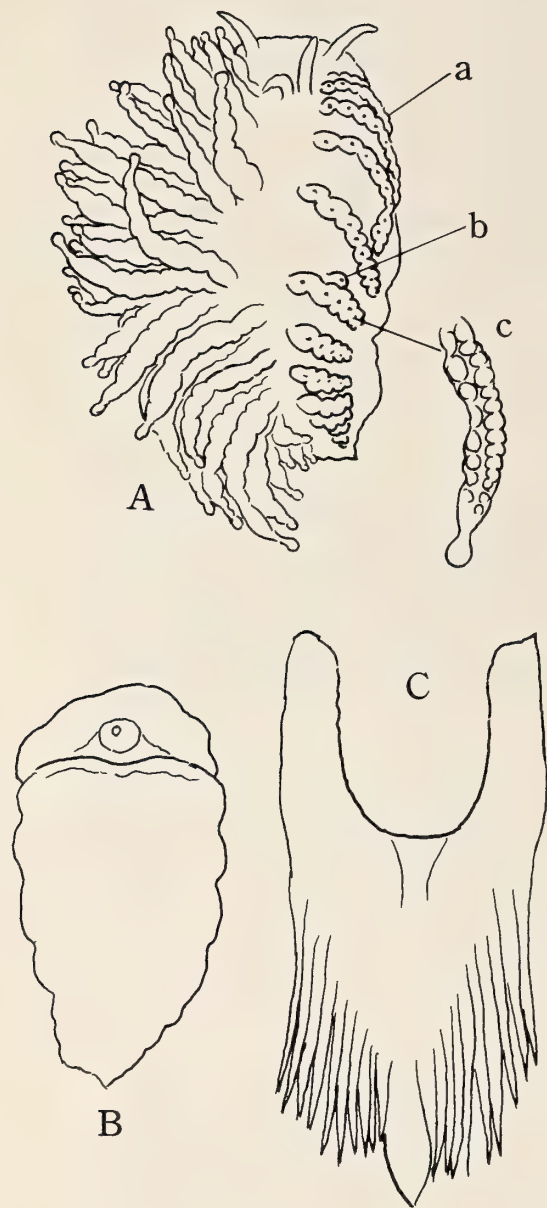


Figure 1

Phestilla lugubris (Palau, 29 Mar. 1940, Kawaguti coll.). A. preserved and contracted animal from dorsal side, length 10 mm; B. the same from ventral side; C. tooth ($\times 360$), the radular formula was $32 \times 0.1.0$, and the denticles numbered 7 to 12 on either side, denticles on jaw edge were missing. a. genital orifices; b. anus; c. branchial papilla tipped with a nipple.

flesh, later starved, and finally the length decreased to 10 mm.

Specimen No. 2. Orange, but slightly paler than the first; length 15 mm. Dissected mainly for the jaws, radula, and penis.

Specimen No. 3. Paler, only slightly tinted orange on the

head and the anterior half of the body; length 7 mm. Figured for the external morphology. Fixed shortly after collecting, and prepared in serial horizontal sections. Gonads not well differentiated.

Specimen No. 4. Juvenile, length 5 mm, a faint orange tinge of body as in Specimen No. 3, but with the branchial papillae relatively fewer in number. Fixed immediately after collecting.

Additional specimen examined for comparison: One large specimen, approximately 25 mm long when preserved and contracted; collected by L. Harris in Kaneohe Bay, Oahu, Hawaii, from a *Tubastraea* colony, 22 June 1967 (see HARRIS, 1968:193).

DESCRIPTION

External form: The animals of Specimens No. 1 and No. 2, though relatively small in size, were mature and capable of spawning (cf. the growth and maturity in *Phestilla* by RUDMAN, 1981:408).

The head is large and tends to form an expanded veil (especially so after preservation). The oral tentacles are short, the rhinophores longer, and both of these simple. The branchial papillae, when fresh, are also simple, smooth (not nodulose) and rounded in section. They are contractile; sometimes they can be extended considerably. Usually they terminate each in a blunt end; at times the extreme tip may be more-or-less instantly elevated. A group of opaque white gland cells lies below the tip of the papillae (see RUDMAN, 1981:402, for *Phestilla lugubris*). In the present species, however, there is no marked formation of the apical nipple of papillae known from *Phestilla lugubris* (RUDMAN, 1981:375). The wall of the liver diverticulum within the branchial papillae is minutely lobated and devoid of zooxanthellae. A cnidosac, present in most aeolids, is missing altogether and is replaced by a sac of clear glandular cells (HARRIS, 1968:194; see also RUDMAN, 1981:402, for the terminal sac of *Phestilla lugubris*).

In Specimen No. 3, there are 10 simple transverse rows of papillae on back margins, of which the foremost 5 rows are ascribed to the right liver (and the left partner) and the rest to the left posterior liver on either side. The papillar arrangement is shown thus: 1, 3, 4, 4, 6; 4, 3, 1, 1, 1, on the right side, and 1, 3, 5, 5, 5; 4, 3, 2, 1, 1 on the left side. The anus and nephroproct are interhepatic as usual. The genital orifices open below the second row of the right liver. Measurements in mm of this animal after RISSO-DOMINGUEZ (1963) were as follows: A 7; Ac 6; C 1; B 1.5; H 1; P 3; T 1; R 1.5.

The branchial papillae, deciduous and normally standing upwardly, are apt to be more crowded in the larger specimens than in the smaller ones. When fresh they do not appear to rest upon raised ridges or cushions (cf. HARRIS, 1968:193; RUDMAN, 1981:375, for *Phestilla lugubris*), but in Specimens No. 1 and No. 2, ridges of papillae were formed transversely by contraction of the body after preservation. The absence of branchial ridges was

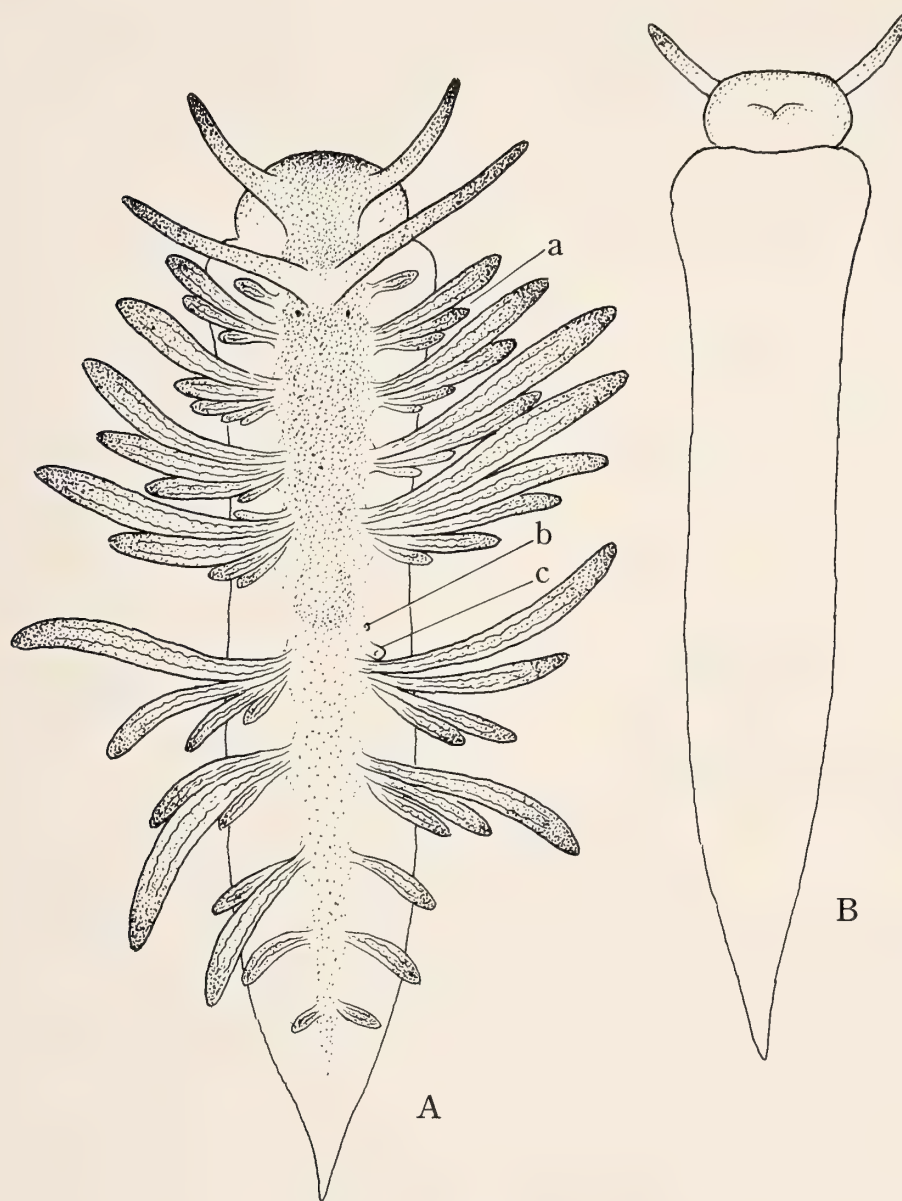


Figure 2

Phestilla melanobranchia (orange form; Specimen No. 3). Living animal from dorsal (A) and ventral (B) sides. The branchial papillae are all drawn in a horizontal plane. a. genital orifices; b. nephroproct; c. anus.

shown by RUDMAN (1981:381) in his small *Phestilla minor* from Tanzania and the Great Barrier Reef, Australia.

The dorso-lateral margins are indistinct. The foot corners are rounded, the sole is expanded flat, and the tail is short.

The animal is able to crawl in an aquarium dish, but usually it stays on the prey corals.

Coloration: Two major colors, black and orange, were

considered by HARRIS (1968) to be displayed by individuals of *Phestilla melanobranchia*. These depended largely on the dominant color pigment of the prey corals, namely *Tubastraea diaphana* (green-black) and *Tubastraea aurea* (orange), which passes into the branchial papillae of the predator. Here it is suggested that the former is a black color form (the type form), and that the latter an orange color form, both of *Phestilla melanobranchia* (see HARRIS, 1968:figs. 2 and 1). But this account should be compared

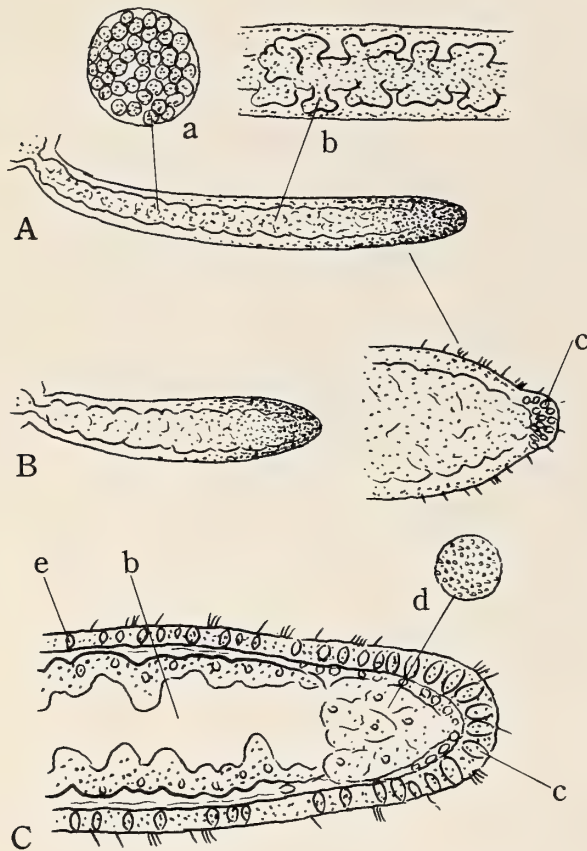


Figure 3

Phestilla melanobranchia (orange form). A. Specimen No. 1, branchial papilla in extended phase, fresh; B. the same in contracted phase, fresh; C. Specimen No. 3, fixed and sectioned branchial papilla ($\times 84$). a. isolated liver cell packed with yellow ferment granules; b. liver diverticulum; c. group of opaque white gland cells, fresh in A and fixed in C; d. terminal sac and an isolated fresh glandular cell composing the sac; e. mucous cell.

with that given by RUDMAN (1981:383) on the brownish form and the white form of *Phestilla minor* living on the same *Porites* colony.

All the specimens I have examined belong to the orange form mentioned above. According to my view, however, the orange hue of these individuals seems to owe for the most part to their natural orange pigmentation of the dermal epithelium. For example, Specimen No. 1 is of the brightest orange appearance while feeding, and this color did not noticeably diminish after it was long starved.

The general color of the body proper is orange. It becomes more prominently bright orange on the head and back, and on the upper half of the oral tentacles, rhinophores and branchial papillae (the orange pigment granules can be seen microscopically in the epithelium of these structures). Mostly hidden by the bright orange pigmentation of the animal, clusters of opaque white dots occur

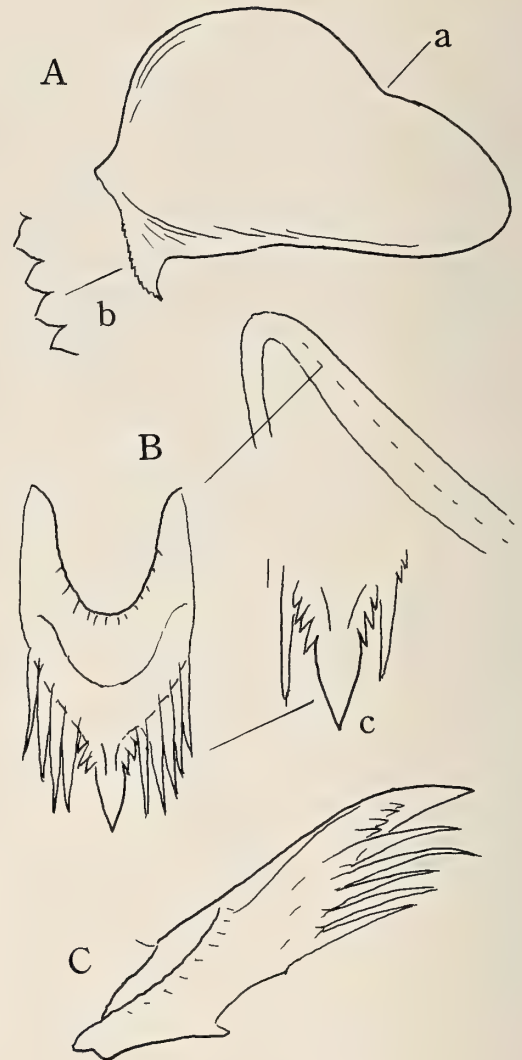


Figure 4

Phestilla melanobranchia (orange form; Specimen No. 2). A. jaw plate ($\times 15$); B. tooth from radular ribbon, dorsal view ($\times 120$); C. the same, lateral view ($\times 160$). a. indentation; b. denticles on jaw edge; c. median cusp.

along the length of the oral tentacles and rhinophores and on the pericardial prominence. The liver diverticulum within each branchial papilla is always tinted yellow owing to the yellow ferment granules which it contains. The foot sole is always colorless.

In Specimen No. 4, which is the youngest of the four specimens, the orange color is visible only on the head, on the back in the anterior half, and the upper half of each of the cephalic structures and branchial papillae. The yellow tint of the liver system is as in the adult specimens.

Internal anatomy: The mouth part and the pharynx are provided each with paired oral glands and paired salivary

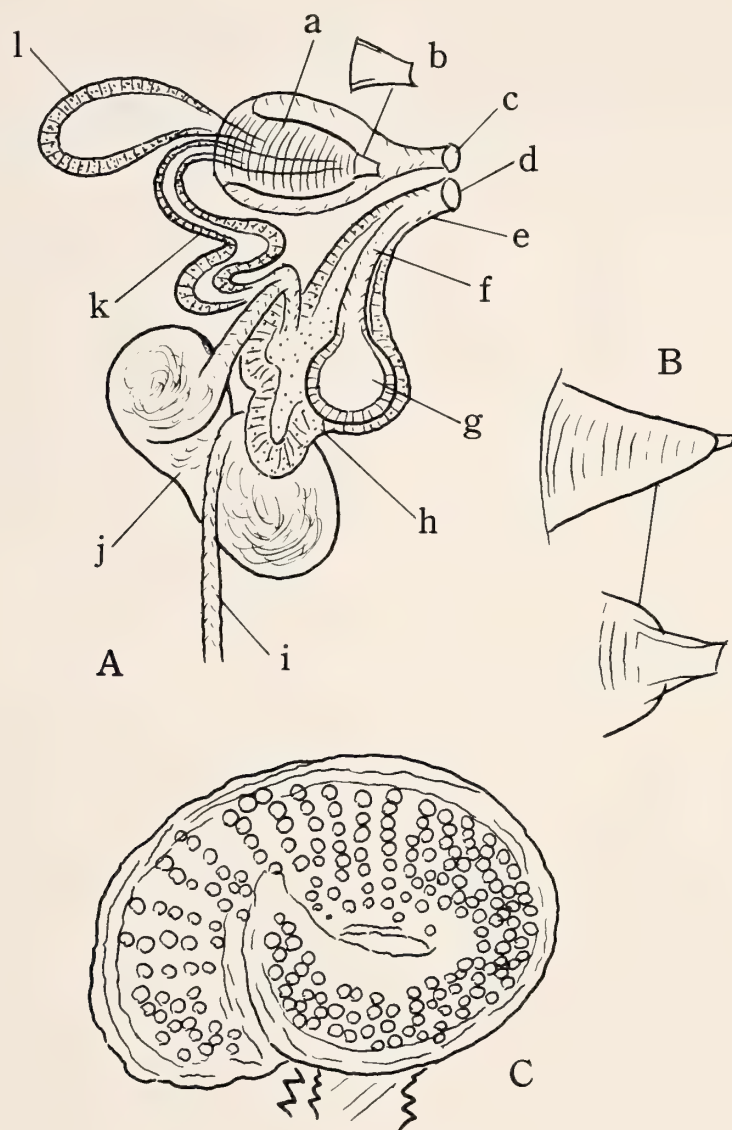


Figure 5

Phestilla melanobranchia (orange form). A. Specimen No. 3, genital organs from dorsal side ($\times 100$); B. Specimen No. 2, penis and apical stylet ($\times 50$); C. Specimen No. 1, egg mass laid on *Tubastraea* skeleton ($\times 10$), the eggs are opaque and faintly tinted yellow. a. penis; b. stylet; c. male orifice; d. female orifice; e. oviduct; f. vagina; g. spermatocyst; h. accessory female gland mass; i. hermaphrodite duct; j. ampulla; k. vas deferens (proximal, prostatic; distal, muscular); l. penial gland.

glands (Specimen No. 3). The liver system corresponds to the simple papillar arrangement of the branchia. The stomach could not be studied exactly. The jaw plate is bilobed postero-dorsally, and the masticatory edge bears a row of about 35 denticles (Specimen No. 2; see also BERGH, 1874:93, pl. 2, fig. 7). The radular formula (Specimen No. 2) is approximately $30 \times 0.1.0$. There are 4 or 5 slender denticles and some secondary ones on either side of the median cusp, which is flanked by minute serrations (see also BERGH, 1874:93, pl. 2, figs. 10–12). All these

denticles and serrations serve to scrape completely the soft flesh of the prey *Tubastraea* out of its hard skeletal hollows.

The genital organs of this species are similar to those of *Phestilla lugubris* (RUDMAN, 1981:381, fig. 6). The conical penis is armed with a short stylet (Specimens No. 2 and No. 3). The penial gland was found empty.

Anatomy of the specimen from Hawaii: This fully matured, dirty brown, preserved specimen (Figure 6) is filled

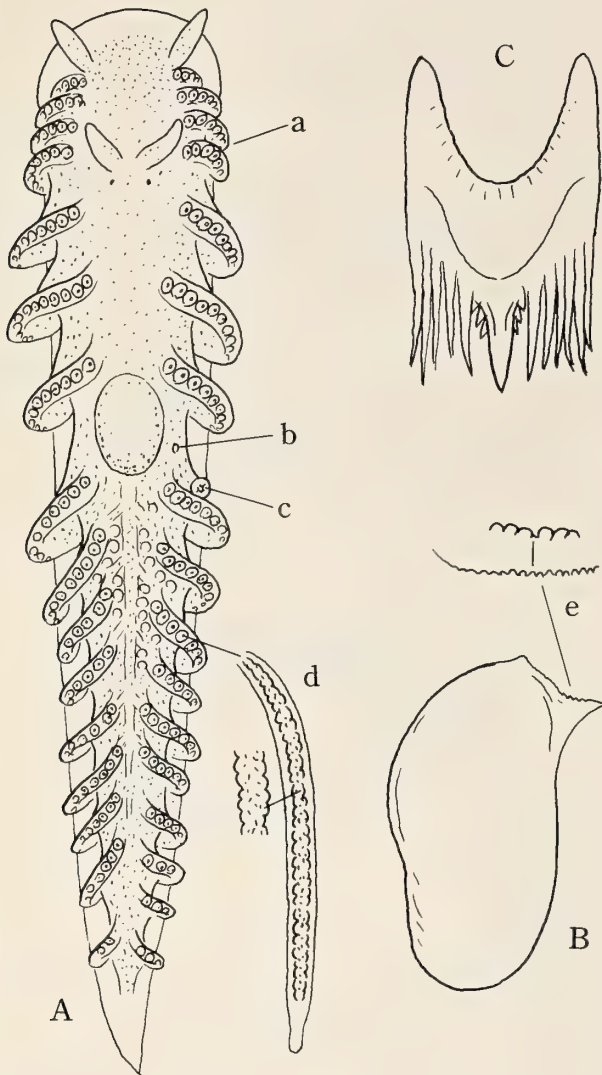


Figure 6

Phestilla melanobranchia (orange form; Hawaii, 22 June 1967, Harris coll.). A. preserved and contracted animal from dorsal side, length 25 mm; B. right jaw plate ($\times 11$); C. tooth ($\times 133$). a. genital orifices; b. nephroproct; c. anus; d. branchial papilla; e. denticles on jaw edge.

internally with paired oral glands in the anterior half and gonadal follicles in the posterior half of the body. Externally the branchial rows form prominent ridges (HARRIS, 1968:193; GOSLINER, 1980:49). There are 7 rows (or ridges) in the right liver (and the partner on the left), and 10 rows in the left posterior liver on either side, the largest rows consisting each of 15 or 16 papillae. The genital orifices are found below the third branchial row of the right liver.

The jaw edge has a row of blunt denticles. The radular formula is $35 \times 0.1.0$. The slender denticles on either side

of the median cusp vary from 5 to 9 in number (the secondary denticles were not well marked). The median cusp is provided laterally with 2 or 3 serrations which are absent in GOSLINER's specimen (1980:fig. 7, A). The penis was not examined (see the armed penis in GOSLINER, 1980: fig. 7, C).

CONCLUSION

The genus *Phestilla* Bergh, 1874, represented by the type species *Phestilla melanobranchia* was clearly shown to possess the digestive and genital organs characteristic of the family Tergipedidae.

This genus is most closely allied to the so-called *Trinchesia* species group of *Cuthona* Alder & Hancock, 1855 (s.l.), in the external morphology with more or less simple transverse rows of branchiae, and in the genitalia provided with a penial stylet. However, *Phestilla* differs markedly from *Cuthona* in the absence of the cnidosacs from the branchiae and also in the formation of the greatly pectinated radular teeth.

ACKNOWLEDGMENTS

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Distributional Records for Terrestrial and Freshwater Mollusca of the Cascade and Coast Ranges, Oregon¹

by

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Abstract. Visitation of 125 Cascade and Coast mountain sites in Oregon during the summer of 1981 yielded records for 15 families, 29 genera, and 45 species of terrestrial and freshwater mollusks. *Pisidium insigne*, *Arion hortensis*, *Prophysaon foliolatum*, and *P. fasciatum* are reported for the first time in Oregon, an undescribed species of *Hesperarion* is discussed, and *Trilobopsis loricata nortensis* is reported in Oregon for the first time since 1897.

INTRODUCTION

THE COAST AND CASCADE mountain ranges divide the state of Oregon into two distinctive molluscan provinces, a lush, moist and narrow western one (west of the Cascade Crest) and a much wider, arid eastern one on the lee side of the Cascade Crest. This general picture partially breaks down along the Columbia River Gorge (DETILING, 1966; LAWRENCE, 1939; LYNOTT, 1966) because Pacific coastal vegetation extends eastward farther than otherwise possible, permitting several species of land snails to extend their ranges eastward a few kilometers along the river. For the most part, however, the bulk of the Oregonian land-snail fauna occurs west of the mountains. The Columbia River itself also acts as a partial barrier, both to dispersal and to genetic mingling. For example, in Washington, *i.e.*, on the north side of the river, *Oreohelix* extends westward along the Columbia River (B. A. BRANSON, 1977), whereas extensive searching on the south side of the river has failed to disclose specimens.

Another relatively distinct botanical, and hence molluscan, region is the southwestern corner of Oregon. In this area, northern Californian vegetation, including coastal redwoods and tanoak, extends into Oregon, creating a habitat that allows certain terrestrial mollusks to extend their ranges northward for a short distance along the coast.

This article reports the results of field work conducted in the Oregon components of the Coast and Cascade ranges during the summer of 1981. It is an extension of work commenced in Washington (B. A. BRANSON, 1977, 1980). About 125 stations were visited in Oregon, although only 82 of these yielded molluscan specimens (see below). The only previous systematic survey of Oregon terrestrial and

freshwater mollusks is that of HENDERSON (1929, 1936), many of his records being reiterated by PILSBRY (1939, 1940, 1946, 1948).

LOCALITIES AND HABITATS

Much of the forest in the Coast Range has been repeatedly and severely slashed and burned, creating very poor molluscan habitats. Our work in these areas resulted principally in negative results. Likewise, practically none of our collecting stations east of the Cascade Crest yielded specimens. There is very little organic soil in that vast region, most of the substrate being of volcanic origin and very dry and porous. Lodgepole and ponderosa pines and other drought-resistant plants are the typical vegetation. Although we did not obtain mollusks at any of them, the following sites are of interest because of biogeographical importance, demonstrating the strong rain-shadow influence of the mountains: 8 sites along Oregon State Route 242 in McKenzie Pass, all in extremely dry, black, unconsolidated lava; 6 sites along Century Drive, a 160-km loop drive west of Bend, up to 1524 m elevation, mostly in insect-devastated lodgepole pines; 6 sites at Paulina Peak, a collapsed volcanic caldera southeast of Bend, mostly in dry lava and pine forests; 8 sites along Oregon State Route 58 east of the Cascade Crest, mostly in dry lava and lodgepole pines; 5 sites around Diamond Lake north of Crater Lake, mostly in dry lava and lodgepole pines; and 10 sites equally distributed on Mount Mazama (Crater Lake National Park) from crest to foot, all in dry lava and pines.

The winter and summer of 1980-1981 were among the driest recorded (U.S. Weather Bureau, Portland, personal communication). This doubtless played a role in reducing our success in mollusk collecting. However, dead shells

¹ Supported by an Eastern Kentucky University Faculty Grant.

were not found in the localities delineated above, forcing the conclusion that the Cascade Crest barrier is a real one.

The sites at which we successfully secured specimens follow. The sites are numbered consecutively, and, in the annotated list, specimens are referred to the sites from which they were collected by these numbers. The figures in parentheses represent the number of specimens secured. The combination of letters and numbers given at each collecting station below, *i.e.*, R 23 E, T 35 S, S 31, are map coordinates obtained from county maps.

1. Chandler Wayside State Park and vicinity of Crooked Creek, U.S. Route 395, R 23 E, T 35 S, S 31, Lake County; 1375 m elevation; western juniper, ponderosa pine, sparse undergrowth, dry lava substrate; 7 June 1981.
2. Grizzly Peak, Fremont National Forest, 9.6 km east of SR 140 via Forestry Road 387, R 12 E, T 38 S, S 7, Lake County; 1890 m elevation; Douglas fir, spruce, aspen, pines, grass; light rain; rocks, soil, lava; 7 June 1981.
3. Grasshopper Flat, Fremont National Forest, 3.2 km via SR 140 west of junction with Forestry Road 387, R 17 E, T 38 S, S 17, Lake County; 1516 m elevation; dry volcanic soil, pines, firs; 8 June 1981.
4. Bly Mountain Pass, Winema National Forest, 16 km north of Bonanza, SR 140, R 11 E, T 37 S, S 22, Klamath County; 1494 m elevation; dry volcanic soil, pine forest with evidence of an old burn; 8 June 1981.
5. Spence Mountain near Upper Klamath Lake, 13.6 km northwest of Klamath Falls, SR 140, R 7 E, T 37 S, S 23, Klamath County; 1391 m elevation; dry pine forest; 8 June 1981.
6. Near Shake Camp Spring, Rogue River National Forest, SR 140, 14.5 km west of Aspen Point, R 3 E, T 37 S, S 5, Jackson County; 1303 m elevation; spruce-fir forest, low undergrowth and ferns; 8 June 1981.
7. North Fork of Little Butte Creek and vicinity, SR 140, R 2 E, T 36 S, S 27, Jackson County; 571 m elevation; soil, marginal oak forest; 8 June 1981.
8. Coast Range, Siskiyou National Forest, 1.6 km northwest of U.S. Route 199, R 8 W, T 37 S, S 13, Josephine County; 457 m elevation; standing and downed oak trees, leaf litter; 9 June 1981.
9. Coast Range, Siskiyou National Forest, U.S. Route 199 at California border, R 9 W, T 41 S, S 14, Josephine County; 366 m elevation; firs, salal, moss, rotting wood; 9 June 1981.
10. Coast Range, 1.2 km northeast of Brookings via North Bank Road, R 12 W, T 39 S, S 23, Curry County; 34 m elevation; below burned over hill along Chetco River, bigleaf maple, ferns, alder, salmonberry, Oregon myrtle (*Umbellularia californica*); 10 June 1981.
11. Coast Range, Siskiyou National Forest, 0.4 km northeast of Loeb State Park, R 12 W, T 39 S, S 30, Curry County; 34 m elevation; coastal redwood, bigleaf maple, tanoak, alder, fir, ferns, huckleberry, Oregon myrtle; 10 June 1981.
12. Low hillside, 1.9 km east of U.S. Route 101, Cape Sebastian Overlook, R 14 W, T 37 S, S 31, Curry County; 230 m elevation; tanoak, Oregon myrtle, fir, ferns, grass; 10 June 1981.
13. Humbug Mountain State Park, Siskiyou National Forest, R 15 W, T 23 S, S 25, Curry County; 49 m elevation; bigleaf maple, Douglas fir, tanoak, fir, ferns, moss; 11 June 1981.
14. Humbug Mountain State Park, Siskiyou National Forest, R 15 W, T 33 S, S 25, Curry County; 183 m elevation, other conditions as at Station 13; 12 June 1981.
15. Humbug Mountain State Park, Siskiyou National Forest, R 15 W, T 33 S, S 25, Curry County; 365 m elevation; other conditions as at Station 13; 12 June 1981.
16. Humbug Mountain State Park, Siskiyou National Forest, R 15 W, T 33 S, S 25, Curry County; 535 m elevation; other conditions as at Station 13; 12 June 1981.
17. Steep bluffs of the Middle Fork of the Coquille River and in the river, 16 km east of Myrtle Point via SR 42, Coos County; bigleaf maple, spruce, fir; 305 m elevation; 13 June 1981.
18. Bear Creek Recreation Area on Middle Fork of the Coquille River and in the river, 43 km east of Myrtle Point via SR 42, Douglas County; 396 m elevation; Douglas fir, spruce; 13 June 1981.
19. Cape Arago at Sunset Bay, near sea level, Coos County; Sitka spruce, skunk cabbage, salmonberry, ferns; 13 June 1981.
20. Honeyman State Park, R 21 W, T 19 S, S 13, Lane County; sea level; Sitka spruce, salal, bigleaf maple, wax myrtle, alder; 14 June 1981.
21. Siuslaw National Forest, 4.8 km east of Florence via Canary Road, R 10 W, T 19 S, S 7, Lane County; 304 m elevation; alder, ferns, decaying wood, skunk cabbage; 14 June 1981.
22. Siuslaw National Forest, 13 km east of Florence via SR 126, along Siuslaw River, R 10 W, T 18 S, S 7, Lane County; 260 m elevation; Douglas fir, bigleaf maple, skunk cabbage, decaying wood; 15 June 1981.
23. Siuslaw National Forest, 24 km east of Florence via SR 126, along Siuslaw River, R 9 W, T 18 S, S 6, Lane County; 304 m elevation; Douglas fir, spruce, decaying wood; 15 June 1981.
24. Sea Lion Caves, R 11 W, T 16 S, S 3, Lane County; 213 m elevation; rocks, salal; 15 June 1981.
25. Cape Perpetua, Siuslaw National Forest campground along Cape Creek and in creek, R 11 W, T 15 S, S 2, Lane County; 183 m elevation; bigleaf maple, Sitka spruce, alder, ferns, moss; 16 June 1981.
26. Cape Perpetua, Siuslaw National Forest Auto Loop Trail, near summit, R 11 W, T 15 S, S 2, Lane County; 472 m elevation; Sitka spruce, may apple, salal, ferns, moss; 16 June 1981.
27. Cape Perpetua, near the terminus of the Siuslaw National Forest Auto Loop Trail, R 11 W, T 15 S, S 2, Lane County; 670 m elevation; spruce, alder, salal, ferns, litter; 16 June 1981.
28. Cape Perpetua, "Devil's Churn," Siuslaw National Forest, R 11 W, T 15 S, S 2; 121 m elevation; Sitka spruce, salal; 16 June 1981.
29. Siuslaw National Forest along Alsea River, approximately 2.4 km east of Tidewater, via SR 34, R 10 W, T 13 S, S 20, Lincoln County; 290 m elevation; bigleaf maple, fir, spruce, ferns, moss, alder; 17 June 1981.
30. Clear-cut forest, 17.7 km southwest of Corvallis, via SR 34, R 7 W, T 13 S, S 1, Benton County; 375 m elevation; young Douglas fir and a few grasses; 17 June 1981.
31. South Beach State Park, R 11 W, T 11 S, S 19, 3.2 km south of Newport, Lincoln County; 61 m elevation; salal, rhododendron; 19 June 1981.
32. Devil's Lake State Park, Devil's Lake, R 11 W, T 6 S, S 35, and in Devil's River, Lincoln County; 64 m elevation; Douglas fir, spruce, salal, ferns, skunk cabbage; 20 June 1981.
33. Swampy area, 1.8 km east of Lincoln City via West Devil's Lake Road, Lincoln County; Sitka spruce, ferns, skunk cabbage, decaying wood; 20 June 1981.
34. Cascade Head Experimental Forest, 4.0 km northeast of

- Otis, R 10 W, T 6 S, S 14, Tillamook County; 335 m elevation; Douglas fir, Sitka spruce, ferns, alder, moss, decaying wood, evidence of an old fire; 21 June 1981.
35. Neskowin Bay area, R 11 W, S 13, Tillamook County; 36.5 m elevation; grasses and sedges; 21 June 1981.
 36. Cape Lookout State Park, R 10 W, T 2 S, S 6, Tillamook County; dead wood, Sitka spruce, skunk cabbage, ferns; 21 June 1981.
 37. Jones Creek Forest Camp, 35 km east of Tillamook via SR 6, Tillamook County; 305 m elevation; clear-cut and burned area, young Douglas fir; 22 June 1981.
 38. Crest of Cape Lookout, R 10 W, T 2 S, Tillamook County; 365 m elevation; decaying wood, Sitka spruce, moss, ferns; 22 June 1981.
 39. Short Beach Trail, Oswald West State Park, Clatsop County; 152 m elevation; undisturbed Sitka spruce forest, western redcedar, hemlock, ferns, moss; 23 June 1981.
 40. Ecola State Park, Clatsop County; 183 m elevation; disturbed Sitka spruce forest; 24 June 1981.
 41. Fort Stevens State Park, Clatsop County; hardwoods, salal, moss, ferns, Sitka spruce, alder; 24 June 1981.
 42. Bradley Wayside, Clatsop State Forest, 6.4 km west of Westport, old U.S. Route 30, Clatsop County; 180 m elevation; wood sorrel, ferns, Douglas fir, decaying wood; 25 June 1981.
 43. Low bluffs, 3.4 km west of Portland via U.S. Route 30, Columbia County; 107 m elevation; volcanic rocks; 25 June 1981.
 44. Latourell Falls and Latourell Creek, R 5 E, T 1 N, S 29, Multnomah County; 61 m elevation; bigleaf maple, firs, moss, volcanic rocks; 27 June 1981.
 45. Wakkeena Falls and Creek, R 6 E, T 1 N, S 9, Multnomah County; vegetation and edaphic conditions as at Station 44; 27 June 1981.
 46. Horsetail Falls and Creek, R 6 E, T 1 N, S 9, Multnomah County; vegetation and edaphic conditions as at Station 44; 27 June 1981.
 47. Ainsworth State Park, R 6 E, T 1 N, S 3, Multnomah County; pines, firs, bigleaf maple, alder, ferns, moss, volcanic rocks and soil; 27 June 1981.
 48. Starvation Creek near Lancaster Falls, R 9 E, T 1 N, S 4, Multnomah County; 33 m elevation; very dry volcanic soil and rocks, pines, few alders along the creek; 28 June 1981.
 49. Dry volcanic slope, 1.6 km below Mayer Roadside via Interstate 80N, R 12 E, T 2 N, S 11, Hood River County; 189 m elevation; ponderosa pine and volcanic rocks; 28 June 1981.
 50. Mount Hood National Forest, Robinhood Campground, R 10 E, T 3 S, S 5, Hood River County; 1082 m elevation; fir, pine, ferns, skunk cabbage; 28 June 1981.
 51. Mount Hood, Mount Hood National Forest, 1.6 km above Government Camp via Timberline Road, R 9 E, T 3 S, S 13, Clackamas County; 1372 m elevation; subalpine fir forest; 30 June 1981.
 52. Mount Hood, Mount Hood National Forest, 4.8 km above Government Camp via Timberline Road, R 8 E, T 3 S, S 18, Clackamas County; 1524 m elevation; subalpine fir forest; 30 June 1981.
 53. Still Creek Campground, Mount Hood National Forest, just off U.S. Route 26 on Forestry Road S 32, R 9 E, T 3 S, S 18, Clackamas County; 1067 m elevation; pine, fir, ferns, moss; 30 June 1981.
 54. Old clear cut at Blue Box Pass, U.S. Route 26, R 9 E, T 4 S, S 20, Wasco County; 1227 m elevation; fir, spruce, much decaying wood; 1 July 1981.
 55. Along Clear Fork of Sandy River, Mount Hood National Forest Road N 12, R 8 E, T 2 S, S 4, Clackamas County; 1042 m elevation; alder, penstemon, mountain mahogany, fir, pine, very dry; 1 July 1981.
 56. Along Hood River just outside Mount Hood National Forest, Forestry Road N 18, R 9 E, T 1 N, S 31, Multnomah County; 613 m elevation; pine, Douglas fir, oak, grass, very dry; 2 July 1981.
 57. Along Hood River, 1.6 km downstream from Station 56, Forestry Road N 18, R 9 E, T 1 N, S 31, Multnomah County; 549 m elevation; alder, bigleaf maple, Douglas fir, ferns, decaying logs; 2 July 1981.
 58. Along Clackamas River, 4.0 km southwest of Ripplebrook Ranger Station via SR 224, R 6 E, T 5 S, S 27, Clackamas County; 488 m elevation; Douglas fir, ferns, decaying wood; 3 July 1981.
 59. Near Clackamas River, 3.2 km southwest of Ripplebrook Ranger Station, SR 224, R 6 E, T 5 S, S 34, Clackamas County; 457 m elevation; dense shade, Douglas fir, ferns, decaying logs; 3 July 1981.
 60. Roaring River, SR 224, R 6 E, T 5 S, S 7, Clackamas County; 304 m elevation; scouring rushes, decaying logs; 3 July 1981.
 61. Near McNeil Forest Camp, Mount Hood National Forest, 6.4 km north of Zig Zag via Forest Road N 12, R 7½ E, T 2 S, S 9, Clackamas County; 496 m elevation; floodplain, decaying logs; 3 July 1981.
 62. Mount Hood Wilderness Area, Mount Hood National Forest, 16 air km northeast of Zig Zag via Ramona Falls Trail, R 8 E, T 2 S, S 24, Clackamas County; 1219 m elevation; Douglas fir, redcedar, moss, ferns, decaying logs; 4 July 1981.
 63. Whispering Falls, R 7 E, T 10 S, S 19, Willamette National Forest, Marion County; 610 m elevation; Douglas fir, hemlock, redcedar, ferns, moss, decaying wood; 5 July 1981.
 64. Lost Prairie, U.S. Route 20, R 6 E, T 13 S, S 34, Linn County; 1013 m elevation; fir-spruce forest; 5 July 1981.
 65. Tombstone Pass summit, U.S. Route 20, R 6 E, T 13 S, S 31, Linn County; 1291 m elevation; fir-spruce forest, decaying logs, heavy snow cover; 5 July 1981.
 66. Banks of Tumalo Creek, Tumalo State Park near Bend, R 10 E, T 18 S, S 8, Deschutes County; 977 m elevation; willows, rank undergrowth, grass, volcanic soil; 7 July 1981.
 67. North boundary of Three Sisters Wilderness, SR 242, R 7 E, T 15 S, S 34, Lane County; 1493 m elevation; firs, grass, decaying logs, rocks; 8 July 1981.
 68. Dead Horse Grade, north boundary of Three Sisters Wilderness, SR 242, R 7 E, T 15 S, S 7, Lane County; 1189 m elevation; Douglas fir, spruce, decaying wood, grass; 8 July 1981.
 69. Proxy Falls, Three Sisters Wilderness, R 7 E, T 16 S, S 23, Lane County; 975 m elevation; Douglas fir, vine maple, redcedar, decaying logs; 8 July 1981.
 70. Northwest boundary of the Mount Washington Wilderness, off Forestry Road 2664, Willamette National Forest, R 5 E, T 14 S, S 33, Linn County; 1069 m elevation; lava, Douglas fir, shrubs; 8 July 1981.
 71. Salt Creek Falls, SR 58, Willamette National Forest, R 5½ E, T 22 S, S 33, Lane County; 1234 m elevation; redcedar, ferns, Douglas fir, maple, decaying wood; 11 July 1981.
 72. Montieth Rock area, SR 58, Willamette National Forest, R 4 E, T 21 S, S 27, Lane County; 670 m elevation; alder, Douglas fir, maple, redcedar, decaying wood; 11 July 1981.
 73. West bank of Hills Creek Lake, R 3 E, T 22 S, S 10, Lane County; 472 m elevation; redcedar, fir, ferns, moss, oak, Pacific madrone; 11 July 1981.

74. North bank of Willamette River between Sacandaga and Indigo Springs, R 4 E, T 24 S, S 11, Forestry Road 21, Willamette National Forest, Lane County; 792 m elevation; redcedar, hemlock, Douglas fir, alder, maple, logging debris, volcanic soil; 12 July 1981.
75. Near southwestern corner of Diamond Peak Wilderness at end of Willamette National Forest Road 393 (off Forestry Road 2154), 9.6 km above Emigrant Creek crossing, R 5 E, T 24 S, S 35, Lane County; 1372 m elevation; volcanic soil and rocks, Douglas fir, white pine; 12 July 1981.
76. Emigrant Creek crossing of Willamette National Forest Road 21, R 5 E, T 24 S, S 21, Lane County; 1115 m elevation; Douglas fir, white pine, alder, maple, decaying wood; 12 July 1981.
77. Fall Creek Reservoir, R 1 W, T 19 S, Willamette National Forest, Lane County; 335 m elevation; 12 July 1981.
78. Suzan Creek State Park, SR 138, banks of Umpqua River, R 2 W, T 26 S, S 24, Douglas County; 285 m elevation; Douglas fir, redcedar, alder, maple, oak; 13 July 1981.
79. Eagle Rock, banks of Umpqua River, SR 138, R 2 E, T 25½ S, S 23, Douglas County; Douglas fir, cedar, alder, maple; 14 July 1981.
80. White Horse Falls, SR 138, R 4 E, T 27 S, S 2, Douglas County; 1156 m elevation; white pine, Douglas fir, rocks; 14 July 1981.
81. Natural Bridge on Rogue River, Rogue River National Forest Road 300, R 3 E, T 31 S, S 16, Jackson County; 954 m elevation; Douglas fir, sugar pine, dry moss; 17 July 1981.
82. Three Horn Camp, Umpqua National Forest, SR 227, R 2 W, T 32 S, S 12, Douglas County; 790 m elevation; Douglas fir, sugar pine, Oregon grapes; 17 July 1981.

ANNOTATED LIST OF TAXA

In the list that follows, specimens are referred to collecting sites by station number, and the number of individuals collected at each site is given in parentheses. Unless otherwise noted, all specimens are in the Eastern Kentucky University Museum of Zoology (EKU).

BIVALVIA

SCHIZODONTA

UNIONIDAE

Margaritifera margaritifera falcata (Gould, 1850)

Collections: 17 (2), 23 (2).

Thriving populations of this bivalve were observed in the Middle Fork of the Coquille River and the Siuslaw River, but only four mature specimens were retained for the ECU museum, all with purple nacre. A representative measured 62.0 mm in length and 31.5 mm in greatest depth.

HENDERSON (1929) reported this mussel as common in many Oregon rivers, and HAAS (1954) took several specimens from the Rogue River at Grant's Pass, Josephine County.

Gonidea angulata (Lea, 1838)

Collections: 17 (4).

Four specimens from the Middle Fork of the Coquille

River (Station 17) were retained for the ECU museum. The species was previously reported from the Umpqua and Silvies rivers (HENDERSON, 1929), the Rogue (HAAS, 1954), and the Walla Walla (COOPER, 1860).

HETERODONTA

SPHAERIIDAE

Sphaerium patella (Gould, 1850)

Collections: 17 (2).

This is one of the most widespread sphaeriids in the Pacific northwest. HENDERSON (1929) reported the species from several Oregon rivers and creeks.

Pisidium insigne Gabb, 1868

Collections: 32 (2).

These specimens, found on the muck bottom of Short Creek running out of Devil's Lake State Park, seem to fit the characteristics of this species better than any other. *Pisidium insigne* has not been previously reported from Oregon.

GASTROPODA

MESOGASTROPODA

PLEUROCERIDAE

Most of the distributional knowledge of this family in the Pacific Northwest is based upon the papers of HENDERSON (1929, 1935a, b, 1936), B. A. BRANSON (1977, 1980), and B. A. BRANSON & BARRETT (1980). In the last-cited paper, we discussed the possibility that GOODRICH (1942) was hasty in relegating HENDERSON's (1935a, b) species to the synonymy of *Goniobasis silicula* and *G. plicifera*. Recently, BURCH (1982) and BURCH & TOTTENHAM (1980) have elected to resurrect the generic designation *Juga* to include all the western U.S. pleurocerids, a name that is probably more in keeping with the concept of subgenus. The nomenclatural problems associated with the family Pleuroceridae should be referred to the International Zoological Commission for decisions under the plenary powers. The strict application of all the changes recommended by BURCH (1982) and others would result in much confusion. Therefore, we elect to utilize the better known and more familiar designations of Goodrich.

Goniobasis (Juga) coquillensis Goodrich, 1935

Collections: 17 (2), 18 (24).

From both sites, the specimens bear two to three rather broad, purplish revolving bands, most obviously on the body whorl and within the aperture. Otherwise, the basic shell coloration is dark brown to mahogany. The sculpturing, spiral and axial, is very well developed. Most of the apices have been eroded, only 4 to 5½ whorls remaining. A sample of 9 shells averaged 17.9 mm (15.5–21.0 mm) in height and 7.9 mm (7.0–9.0 mm) in greatest diameter.

Goniobasis (Juga) hemphilli dallesensis Henderson, 1935

Collections: 13 (2), 44 (4), 46 (4).

The specimens from Station 13, a small, clear creek at the base of Humbug Mountain, are far out of range for this race, but their characteristics are nearly identical to those presented by HENDERSON (1935a, b), as confirmed by comparison with topotypes. The spiral sculpture is very faintly developed, whereas the remainder of the shell is nearly smooth. There are two or three purplish bands on the body whorl.

Goniobasis yrekaensis Henderson, 1935

Collections: 7 (27).

These dark mahogany-brown, slender shells are heavily sculptured with radial and spiral lines, top to bottom. A sample of 5 shells averaged 16.3 mm (15.0–17.5 mm) in length, 6.7 mm (6.5–7.0 mm) in width, and had apertures that averaged 6.9 mm (6.6–7.1 mm) by 4.5 mm. The population in this stream is very large.

Goniobasis (Juga) silicula (Gould, 1847)

Collections: 25 (7), 77 (13).

All specimens were more or less typical in coloration and sculpturing except for moderate banding at Station 25.

HYDROBIIDAE

The generic designation utilized herein is that of TAYLOR (1966). BURCH (1982) utilized *Fluminicola*, as have many other former authors.

Lithoglyphus virens (Lea, 1839)

Collections: 17 (2).

BASOMMATOPHORA

ANCYLOPLANORBIDAE

The family and generic designations used herein are those of HUBENDICK (1978).

Planorbula (Menetus) opercularis (Gould, 1847)

Collections: 32 (2).

This is the dominant mollusk in the discharge creek at Devil's Lake.

PHYSIDAE

HENDERSON (1929, 1936) presented many records for physid snails in Oregon but little has appeared in the literature since then. BURCH (1982) and BURCH & TOTTENHAM (1980) use the generic epithet *Physella* rather than *Physa*.

Physa gyrina ampullacea Gould, 1855

Collections: 7 (1), 32 (2).

BURCH (1982) and BURCH & TOTTENHAM (1980) reduced *P. ampullacea* to subspecific status.

Physa traski (Lea, 1864)

Collections: 1 (1).

A single specimen was retained for the record. However, the Crooked Creek population is a very large one. No other mollusks were observed in the stream.

CARYCHIIDAE

Carychium occidentale Pilsbry, 1891

Collections: 17 (2), 29 (8), 47 (3), 77 (10).

Practically all these specimens were removed from hardwood leaf litter. PILSBRY (1948) reported specimens from Portland and Multnomah, Clackamas and Clatsop counties, and HENDERSON (1929) took specimens from Springfield Junction and reported (1936) upon specimens at Stanford University from Astoria, Salem, and Portland. A sample of seven individuals averaged 2.1 mm (2.0–2.2 mm) in length, 0.96 mm (0.8–1.0 mm) in greatest diameter, and 5½ (5¼–5½) whorls.

STYLOMMATOPHORA

HELMINTHOGLYPTIDAE

Monadenia fidelis (Gray, 1834)

Collections: 8 (4), 10 (5), 11 (4), 13 (1), 15 (5), 16 (1), 17 (16), 18 (1), 19 (1), 23 (1), 44 (1), 48 (1), 49 (3), 73 (2), 74 (2), 77 (1), 78 (5), 81 (1), 82 (1).

The Columbia River gorge interrupts the Cascade Crest weather barrier, allowing rain clouds to sweep moisture-laden air masses farther inland than would be possible otherwise, creating gradations of plant life (DETLING, 1966; LAWRENCE, 1939; LYNOTT, 1966). There is a corresponding color and banding variation in *M. fidelis* populations distributed along the gorge (R. M. BRANSON, 1983). The climatic amelioration, of course, allows this and other species of snails and slugs to penetrate considerably farther inland than elsewhere in the Cascade Mountain region.

Representative average measurements of adult shells (*i.e.*, with reflected peristomes fully formed) from the principal biotopes follow: coastal (N = 16)—diameter: 31.7 mm (20.2–41.1 mm); height: 25.9 mm (18.0–39.0 mm); whorls: 6+ (5½–6¾); Columbia River gorge (N = 2)—diameter: 30.8 mm (28.2–33.5 mm); height: 19.2 mm (16.5–22.0 mm); whorls: 5½–6¾; upland sites (N = 6)—diameter: 30.3 mm (23.5–34.5 mm); height: 19.8 mm (14.6–24.0 mm); whorls: 6½ (5¾–6¾). The largest specimens were obtained from extreme southwestern Oregon (vicinity of Harris Beach and Loeb State Park). However, the coastal shells tend to have higher spires (Diameter/Height ratio averages 1.4) than those from Columbia River gorge or upland sites (D/H ratio averages 1.55).

Additional Oregon distribution records may be found in PILSBRY (1939), HENDERSON (1929, 1936), HAAS (1954), WALTON (1970), and ROTH (1981).

POLYGYRIDAE

Triodopsis germana (Gould, 1851)

Collections: 7 (5), 13 (1), 23 (1), 29 (1), 36 (1), 42 (1), 77 (1), 78 (8).

The specimens from Jackson County (Station 7) are sparsely hirsute and, in general, match the diagnosis of *T. germana vancouverinsulae* (Pilsbry & Cooke, 1922) (PILSBRY, 1940). These specimens average 8.8 mm (8.5–9.0 mm) in diameter, 5.3 mm (5.0–6.0 mm) in height, and have 5–5½ whorls. Specimens from coastal sites, by contrast, bear many fine, close-set hairs. Many specimens are only minutely perforate, and the parietal tooth is well-developed; lip teeth are sometimes lacking. Shells from coastal areas average 9.1 mm (7.7–11.0 mm), 6.3 mm (5.5–7.5 mm) in height, and have 4¾–5½ whorls. Specimens from inland sites, such as those from headwater sections of the Umpqua River (Station 78), average somewhat larger, 11.6 mm (10.2–13.0 mm) in diameter, 7.4 mm (7.0–8.5 mm) in height, with 5½–6 whorls.

Vespericola columbiana (Lea, 1838)

Collections: 6 (3), 10 (7), 12 (4), 13 (6), 15 (4), 16 (5), 17 (3), 19 (8), 20 (2), 21 (1), 22 (13), 23 (1), 24 (9), 27 (3), 29 (4), 31 (1), 33 (5), 34 (3), 36 (1), 37 (1), 38 (3), 39 (1), 41 (8), 43 (1), 44 (11), 47 (2), 49 (1), 50 (3), 55 (3), 57 (1), 58 (1), 61 (1), 63 (1), 64 (1), 69 (1), 70 (1), 72 (4), 73 (1), 74 (4), 77 (2), 78 (5), 79 (2), 81 (3), 82 (3).

This is one of the most widely distributed species of land snails in the Pacific northwest (B. A. BRANSON, 1977, 1980; PILSBRY, 1940; HENDERSON, 1929, 1936), particularly in Oregon west of the Cascade Crest. In Oregon, it is also a rather variable species as one progresses inland, although in the Coast Range and on the western slopes of the Cascades most specimens are readily assignable to *V. columbiana pilosa* (Henderson, 1928). Specimens from inland sites tend to be slightly larger in diameter. Average measurements for mature shells secured along the coast are: 13.7 mm (11.2–17.5 mm) in diameter, 9.2 mm (7.5–11.5 mm) in height, with 5½–6½ whorls. A few of these shells lack apertural teeth. At inland sites (Stations 55, 61, 73–74, 78–79) average measurements were: 16.0 mm (14.0–18.0 mm) in diameter, 11.1 mm (10.0–12.2 mm) in height, with 5¾–6½ whorls. These latter shells tend to be less hirsute than ones from coastal areas.

Specimens from the Columbia River gorge, from the relatively dry habitats in Mount Hood National Forest along the Hood River in Multnomah County, and from sites along the Clackamas River in Clackamas County differ considerably from those discussed above. Although partially covered by a columellar reflection of the lip, the umbilicus is obviously enlarged, 13–15% of the total diameter of the shell. The reflected, white peristome is wide and nearly flat, and the aperture, mostly because of the angular periphery, has a shape reminiscent of that seen in some depressed forms of *Monadenia*, i.e., it is elongated horizontally. The matt shell surface bears very short, stiff and sparse periostracal processes, spirally arranged on the base. Average measurements of mature shells are: 16.5 mm (15.0–18.5 mm) in diameter, 11.1 mm (10.5–11.5 mm) in height, with 5¾–6½ whorls. This is probably the

form PILSBRY (1940) referred to *V. columbiana latilabrum* Pilsbry, 1940. The marked differences in the shells suggest that *latilabrum* probably deserves full-species designation, but that will have to be verified by careful analysis of the genital anatomy.

Trilobopsis loricata nortensis (Berry, 1933)

Collections: 10 (1).

HAAS (1954) indicated that his collection of two specimens from the redwoods west of the Hiouchi Bridge was the first record for this subspecies since the original description. HENDERSON (1936) did not collect it but discussed ANDRUS' (1897) report from Douglas County, Oregon, under the epithet *T. loricata loricata*. PILSBRY (1940) stated that he was "temporarily referring Andrus specimens to *T. l. nortensis*." Thus, the single specimen reported here appears to be the first verified report of the species in Oregon since 1897.

The collecting locality is, of course, very similar to the type locality in Del Norte County, California, including the presence of Coast redwoods. The upper surface of the shell bears strong spiral sculpture crossed by moderately strong radial sculpture. The base is marked by well-developed spiral sculpture, and there is a plethora of raised, crescent-shaped tubercles. There are two widely spaced lip teeth and a relatively large, white and slightly sinuous parietal tooth. *Trilobopsis loricata nortensis* probably deserves full-species recognition, but this needs to be verified by features of the soft anatomy.

HAPLOTREMATIDAE

Haplotrema vancouverensis (Lea, 1839)

Collections: 10 (3), 11 (2), 12 (7), 14 (4), 15 (3), 16 (3), 17 (7), 22 (5), 23 (2), 25 (3), 26 (1), 27 (3), 29 (6), 37 (1), 38 (5), 39 (2), 42 (2), 44 (1), 45 (2), 47 (4), 53 (1), 57 (1), 58 (1), 60 (1), 61 (1), 62 (2), 63 (3), 69 (1), 72 (4), 73 (1), 77 (2), 79 (2), 82 (1).

Haplotrema sportella (Gould, 1846)

Collections: 11 (2), 12 (1), 13 (11), 15 (7), 16 (1), 17 (7), 19 (1), 21 (1), 22 (11), 24 (3), 26 (1), 27 (7), 29 (4), 30 (3), 33 (2), 34 (2), 37 (1), 41 (10), 42 (2), 44 (16), 45 (7), 47 (6), 48 (1), 52 (2), 53 (1), 56 (1), 57 (4), 58 (1), 59 (2), 61 (2), 72 (4), 74 (6), 76 (2), 77 (2), 78 (1), 80 (2).

As stated previously (B. A. BRANSON, 1977), *H. sportella* seems to be a complex of at least two species. The whole west coast complex is in need of revision, utilizing detailed anatomical features and, perhaps, the results of electrophoretic analysis.

Specimens from Benton County, Oregon (Station 30) are much greener than ones from most other localities, and the shell is very solid, mostly because of a thick pearly layer within.

Haplotrema sp.

Collections: 9 (2).

These shells, 19.0 mm in diameter, are palish green in

color and are very smooth. The aperture is nearly transverse. In general configuration, they are strongly reminiscent of *H. keepi* (Hemphill, 1890) from Redding in Shasta County, California. Additional collecting at this locality, which is at the California border, is required before specific diagnosis can be attempted.

ZONITIDAE

Representatives of six genera and nine species were collected.

Euconulus fulvus (Müller, 1774)

Collections: 3 (4).

These shells measured 3.0–3.2 mm in diameter and had 5–5+ whorls.

Nesovitrea binneyana occidentalis (H. B. Baker, 1930)

Collections: 41 (3).

These specimens were living in hardwood leaf litter on sandy soil.

Pristiloma cf. chersinella (Dall, 1886)

Collections: 17 (1).

The single waxen-white specimen, measuring 2.0 mm in diameter with three whorls, seems closer to *P. chersinella* than to any other *Pristiloma*. This species was previously reported from the vicinity of Upper Klamath Lake in Oregon (BAKER, 1931; HENDERSON, 1936). However, *P. wascoense* (Hemphill, 1911) is also known from Oregon near Salem (BAKER, 1931) and the Willamette Valley (PILSBRY, 1946), although we were unable to recognize that species in our collections.

Pristiloma lansingi (Bland, 1875)

Collections: 13 (1), 41 (4), 47 (2), 77 (5).

The imperforate shells are pale amber in coloration and are transparent. Growth striae are nearly lacking. A very low but well-developed denticulate ridge occurs immediately inside the aperture on the lower and middle lip. The shells measure 2.0–2.5 mm in diameter and have 4½–5½ whorls. PILSBRY (1946) and HENDERSON (1929) presented additional localities in Oregon.

Pristiloma johnsoni (Dall, 1895)

Collections: 13 (1), 23 (1), 48 (1), 75 (1), 78 (1).

The last whorl in these waxen-white shells is nearly twice as wide as the preceding one and the spire is strongly depressed. Measurements: 2.4–2.8 mm in diameter, with 3½ whorls.

Zonitoides arboreus (Say, 1816)

Collections: 74 (1), 78 (1).

Zonitoides arboreus is not a particularly common species in the Pacific northwest, although it is apparently locally abundant in the mountains farther east (B. A. BRANSON, 1977). The two specimens reported here measure 3.0–4.3 mm in diameter and have 3½–4+ whorls.

Zonitoides nitidus (Müller, 1774)

Collections: 5 (1).

There are few records for this snail on the west coast. In Oregon, it was known previously from Astoria (PILSBRY, 1946).

Striatura pugetensis (Dall, 1895)

Collections: 17 (1), 41 (2), 58 (1).

There are few published records for this minute species in Oregon. PILSBRY (1946) recorded it from Clackamas, Clatsop, Klamath, and Multnomah counties, and HENDERSON (1929, 1936) from Springfield and Elkhorn, Oregon. Our specimens measured 1.2–1.6 mm in diameter and were less than 0.5 mm in height; there are 2¾–3¼ whorls.

Vitrina alaskana (Dall, 1905)

Collections: 1 (5), 2 (3), 7 (3), 66 (1).

All of our specimens were found east of the Cascade Crest in very dry habitats, mostly under basaltic rocks. All represent new distribution records within Oregon; the previous reports are from Willamette, Umatilla, and Klamath counties (PILSBRY, 1946), all of which are also dry habitats.

TESTACELLIDAE

Testacella haliotidea Draparnaud, an agnathous shell-bearing slug from western Europe (PILSBRY, 1946), was reported from greenhouses in Clackamas County (BRUCE, 1950) and Salem and Corvallis, Oregon (HANNA, 1966).

ENDODONTIDAE

Punctum randolphi (Dall, 1895)

Collections: 66 (1).

This locality, a new distributional record in Oregon, lies east of the Cascade Crest in very dry country. However, the specimen was removed from moist, decaying wood on the banks of Tumalo Creek. All other published Oregon records are from west of the Cascade Crest (PILSBRY, 1948).

LIMACIDAE

In addition to the species reported here, PILSBRY (1948) reported *Limax maximus* Linnaeus from Salem and *Milax gagates* (Draparnaud) from Clackamas, Benton and Douglas counties.

Deroceras reticulatum (Müller, 1774)

Collections: 7 (1), 66 (1).

Both individuals are more or less typical specimens, and both were taken from areas with a history of recent human disturbance. Several coastal and Columbia River sites were given by PILSBRY (1948). This species is a rather serious pest in Oregon strawberry and truck crops (CAPIZZI, 1960a) and grains (CAPIZZI, 1961).

Deroceras laeve (Müller, 1774)

Collections: 4 (5).

This site is a very dry pine forest near Klamath Lake, a rather unusual habitat for this slug.

PUPILLIDAE

As pointed out many years ago (HENDERSON, 1929), the family Pupillidae is rare to uncommon in the Pacific northwest. Although we searched diligently in many habitats at all elevations from sea level to the Cascade Crest and at and above timberline on the high volcanoes, we were unable to secure representatives of the family.

VALLONIIDAE

Vallonia cyclophorella Sterki, 1892

Collections: 1 (83), 3 (3), 4 (15).

Although a common species on the lee side of the mountains, *V. cyclophorella* appears to be very scarce or even lacking west of the Cascade Crest in Oregon. Measurements: 2.7–3.0 mm in diameter; whorls 3½–3¾.

ARIONIDAE

Although HANNA (1966) indicated that *Arion fasciatus* Nilsson was common in the vicinity of Corvallis we did not secure specimens in that area.

Arion ater (Linnaeus, 1758)

Collections: 19 (3), 20 (1), 21 (4), 31 (6), 32 (3), 35 (1), 36 (4), 41 (5), 47 (1).

These numbers are, of course, in no manner representative of population sizes. Whenever encountered, *A. ater* was always present in enormous numbers, often at destructive levels, as also was reported by CAPIZZI (1960b). At Stations 31 and 32, thousands of individuals per hectare were observed, principally at dusk and after sunset; *A. ater* is principally a nocturnal slug (LEWIS, 1969). As far as we can tell, REHDER (1947) was first to report this European exotic from Oregon.

Arion hortensis (Férussac, 1819)

Collections: 32 (8), 41 (2).

This slug, another European exotic, apparently has not heretofore been reported from Oregon. This diagnosis should be substantiated.

Prophysaon andersoni (J. G. Cooper, 1872)

Collections: 9 (2), 13 (1), 15 (1), 17 (4), 18 (1), 19 (2), 26 (1), 32 (2), 36(2), 41 (5), 51 (2), 52 (1), 53 (2), 54 (2), 59 (1), 63 (4), 64 (2), 65 (3), 67 (4), 68 (1), 72 (2), 77 (1), 78 (3), 79 (4), 80 (1).

This handsome little slug is more widely distributed in Oregon than any other member of the genus, often being collected with *P. caeruleum* at 1500 m elevation or above. A favored habitat is decaying logs and standing stumps.

Prophysaon foliolatum (Gould, 1851)

Collections: 14 (1), 42 (4).

These are the only published records for this slug from Oregon. Although both collecting sites are worthy of note, the Humbug Mountain station is of particular interest because of its distance from the principal center of distribution.

Prophysaon caeruleum Cockerell, 1890

Collections: 59 (1), 60 (1), 63 (1), 75 (1), 76 (1), 81 (1).

Known previously only from localities in Portland, Oswego, and Corvallis (PILSBRY, 1948), this bright-blue to bluish-gray slug is one of formidable habitats. We took specimens from high woodlands where the snow lingers well into July. It is also one of the few slugs encountered in dry, volcanic areas such as those at the Diamond Peak Wilderness (Station 75) and the Rogue River National Forest (Station 81).

Prophysaon dubium Cockerell, 1890

Collections: 7 (1).

In life, this specimen was dark bluish-gray above, and the narrow, rugose, undivided sole was grayish-white. The mantle, the same color as the body with three indistinct, blackish, chevron-like marks at the anterior end, is smooth above, but bears very small papillae on the sides. The body tapers posteriad, and bears deep, longitudinal grooves; shallow, transverse grooves periodically cut across the longitudinal ones. There is no mucous pore. Preserved measurements are: total length—16.0 mm; mantle length—6.0 mm.

The only previous records for the species in Oregon are from Portland, Oswego, and Corvallis (PILSBRY, 1948), and "Oregon" (WEBB, 1961).

Prophysaon vanattae Pilsbry, 1948

Collections: 50 (2), 52 (2), 57 (3), 59 (1), 61 (8).

Apparently restricted in distribution to northwestern Oregon and Washington, this slug is often confused with *P. fasciatum*. The red phase discussed by PILSBRY (1948) and B. A. BRANSON (1980) is rare to lacking in most of the Oregon range, most of the specimens being similar to those from the Olympic Peninsula (B. A. BRANSON, 1977). Individuals from the population on and near Mount Hood are often nearly black, other color-pattern elements being obscured.

Prophysaon fasciatum Cockerell, 1890

Collections: 44 (1), 62 (1).

These two specimens are of the kind referred to as *P. f. obscurum* Cockerell by PILSBRY (1948), who stated that the northern race (Washington) was probably a distinct species, based upon genital differences. These are the first published records for Oregon.

Hesperarion species

Collections: 38 (2).

Prior to this report, the genus *Hesperarion* was thought to be restricted in distribution to California around and south of San Francisco (GREGG, 1961; MEAD, 1943; PILSBRY, 1948) and Tehama County (LANGE, 1944). Our record represents a significant range extension for the genus.

This apparently unknown slug species differs from all other members of the genus *Hesperarion* by characters of the genitalia and features of the body sculpturing on the

head and body, by the raised hump-like area beneath the mantle, and by color pattern. It is most closely related to *H. hemphilli* (W. G. Binney) but differs from that species in the decidedly reddish pigmentation, in having the black spots of the body arranged in a definite pattern and rows, in having a larger caudal pit with a down-turned ventral portion, and in possessing a massive triangular and constricted penis. Additional differentiating features will probably be discovered in the radula, genitalia, and musculature when additional specimens become available. A voucher specimen was deposited at the Field Museum of Natural History (FMNH 198763) in Chicago.

Hemphillia malonei (Pilsbry, 1917)

Collections: 42 (2), 51 (1), 53 (9).

This species appears to be restricted to the Columbia River gorge and Mount Hood regions of Oregon. Previous distribution records (Clackamas, Multnomah, and Hood River counties) were given by KOZLOFF & VANCE (1958).

Hemphillia cf. burringtoni (Pilsbry, 1948)

Collections: 39 (1 immature).

This specimen is indistinguishable from specimens secured from the Olympic Peninsula. However, the area needs to be more thoroughly searched for mature specimens before this species is definitely added to the Oregon fauna.

Ariolimax columbianus (Gould, 1851)

Collections: 10 (1), 13 (2), 16 (1), 17 (2), 18 (1), 19 (3), 20 (1), 21 (3), 22 (5), 23 (1), 24 (4), 25 (1), 26 (1), 28 (1), 29 (2), 30 (1), 31 (2), 34 (2), 35 (1), 36 (1), 38 (2), 39 (1), 40 (1), 42 (4), 44 (1), 45 (1), 47 (1), 48 (1), 62 (1), 68 (1), 70 (1), 71 (1), 73 (2), 76 (2), 77 (1), 78 (3).

Although both maculated and spotless color morphs occur throughout the range of this widespread slug, Oregonian populations appear to be less variable than those farther north in Washington and on the Olympic Peninsula (B. A. BRANSON, 1977). MEAD (1943) provided a detailed discussion of the genus *Ariolimax*.

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The Biology of the Northeastern Pacific Turridae. IV. Shell Morphology and Sexual Dimorphism in *Aforia circinata* (Dall, 1873)

by

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Abstract. The shell morphology of the boreal deep-water species *Aforia circinata* is examined, and a pronounced dimorphism in sexually mature animals is described. Mature females have a canal-like notch, which is lacking in males, midway down the outer lip. The notch is similar to, but smaller than the siphonal canal, and arises abruptly from a low ridge at an approximate shell length of 76 mm. The notch may function as an auxiliary siphonal canal during oviposition. No other sexual differences in shell shape of immature animals could be demonstrated, although small males are more variable in some measurements than are small females, or large animals of either sex. Healed shell fractures are common, and are probably due to attempted predation by crabs.

INTRODUCTION

WITH THE EXCEPTION of the cephalopods, sexual dimorphism has not been commonly demonstrated in mollusks. In prosobranch gastropods, sexually determined size dimorphisms have been reported in several lineages: for *Cypraea* (CLENCH & ABBOTT, 1943); *Fasciolaria* (WELLS, 1970); *Mitra* (CHESS & ROSENTHAL, 1971); *Thala* (MAES & RAEHLE, 1975); *Neptunea* (MACINTOSH & PAUL, 1977); *Buccinum* (TEN HALLERS-TJABBES, 1979); and *Drillia*, *Strictispira*, *Pilsbryspira* (MAES, 1983). That females are larger than males within the stenoglossa may be a general trend that goes unnoticed due to the relatively large sample sizes needed to determine a statistically significant difference in the mean adult size between the sexes of any given population. Although MAES (1983) demonstrated size differences in four species of Caribbean turrids, no size differences have been observed in any northeastern Pacific turrids examined to date (SHIMEK, 1983a, b, c), even though sufficiently large samples have been examined in detail.

Sexually correlated differences in shape are even less common. The sexes of *Voluta musica* Linné, 1758, and *Voluta ebraea* Linné, 1758, are sufficiently different to be easily distinguished (CLENCH & TURNER, 1964), but whereas there are slight sexual differences in the shell

shapes of *Buccinum undatum*, sophisticated mathematical and measuring techniques are needed to demonstrate them (TEN HALLERS-TJABBES, 1979). *Neptunea* species also have a size dimorphism similar to that shown in *Buccinum undatum* (MACINTOSH & PAUL, 1977) and similar subtle shape differences may occur. Sexual shell-shape differences have not been reported in the toxoglossa, although "odd" shapes at variance to the typical shell shape have been noted for several tropical turrids (POWELL, 1964, 1969).

The northeastern Pacific boreal turrid *Aforia circinata* (Dall, 1873) is seldom collected, and ecologically poorly known; data on diet, habitat, reproduction, and population biology are lacking. During examination of specimens of this species, several individuals were found exhibiting the "odd" shape (Figure 1) described and figured by POWELL, 1969. I attempted to correlate this shape with other observable features of the organisms.

A characteristic of the immense prosobranch family Turridae is the presence of a secondary or anal notch. The position of this notch varies with the subfamily of turrids examined, but it is typically very near the shoulder. It never forms a "spout" nor has a siphonal canal-like appearance.

The hypothesis tested was that the odd shape, a distinct "tertiary" notching of the outer lip, similar in shape to the siphonal canal, is randomly distributed throughout the species. The tertiary notch might be related to sex and/or size (and presumably age).

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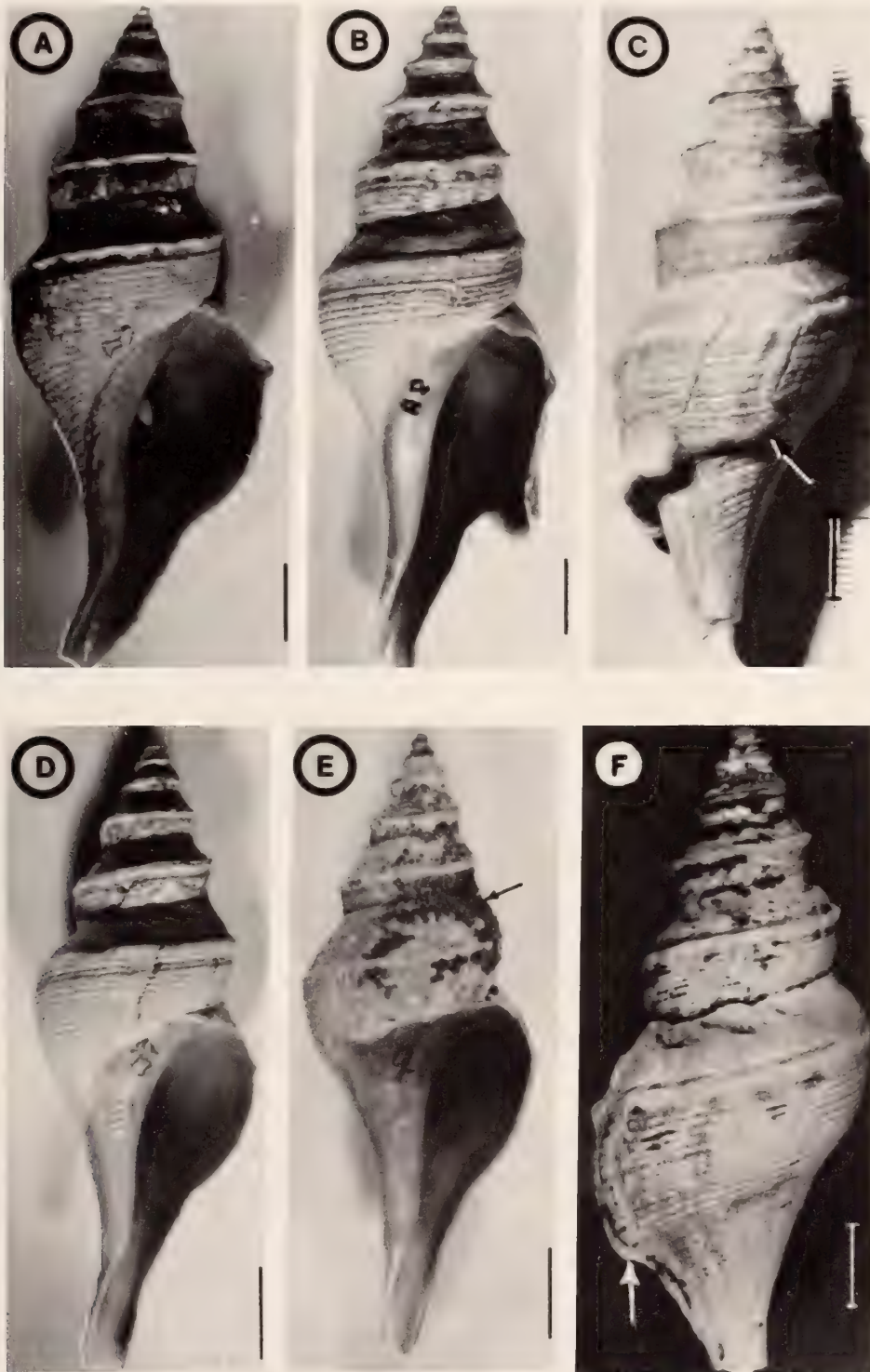


Figure 1

Aforia circinata. Scale bars = 1 cm. A. Mature male. B. Mature female; note tertiary notch on outer lip (compare with Figures 1A and 1E). C. Mature female (different from the one illustrated in Figure 1B); arrow indicates initiation of notch; note healed fractures, and how the notch is displaced after subsequent break. D. Immature male. E. Immature female; material on shell (arrow) is the remains of a hydractiniad hydrozoan; virtually all shells were covered with this material, and it had to be removed with the underlying periostracum to examine the shell. F. Mature male with a low ridge (arrow); females often had similar, albeit more pronounced, ridges.

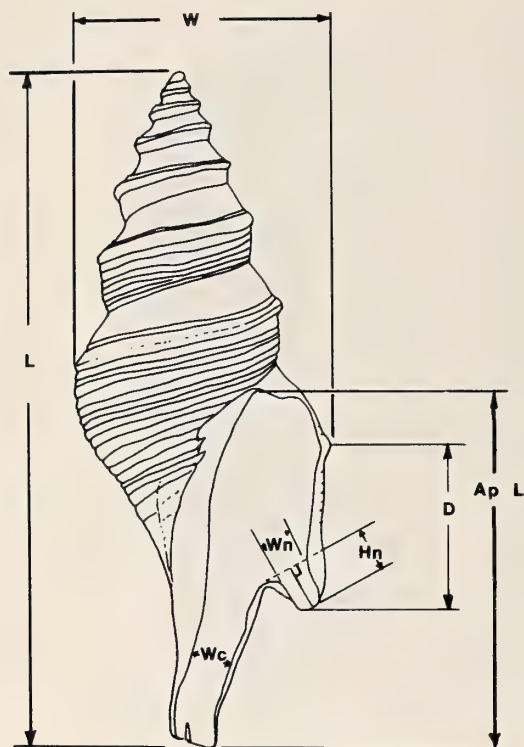


Figure 2

Measurements of *Aforia circinata*. L, shell length; W, shell width; Ap L, aperture length; D, distance from the shoulder carina; Wc, width of the siphonal canal; Wn, width of the tertiary notch; Hn, height of the tertiary notch.

MATERIALS AND METHODS

The specimens of *Aforia circinata* examined were collected from two localities in the Bering Sea, 59°20.3'N, 173°44.3'W, and 58°21.2'N, 172°19.0'W, with a 400-mesh Eastern Otter Trawl; thus, no specimens less than 50 mm long were collected. The first site, at a depth of 109 m, sampled on 25 June 1980, yielded 30 specimens; the second, at a depth of 102 m, sampled on 23 June 1980, provided seven specimens. The animals were preserved immediately in 95% ethanol. Animals from both populations were pooled for all analyses.

During examination, the snail's body was removed from the shell, the sex was determined, and an arbitrary estimate of maturity was obtained by examining the secondary sexual organs. In mature males, the penis is large, at least twice as long as the width of the mantle cavity. Males were classified as immature if the penis length was less than or equal to mantle-cavity width at the base of the penis. In mature females, the capsule gland is large and robust; generally it is three to five times the diameter of the nearby hindgut. Consequently, females were classified as immature if the capsule gland was the same diameter or smaller than the nearby hindgut.

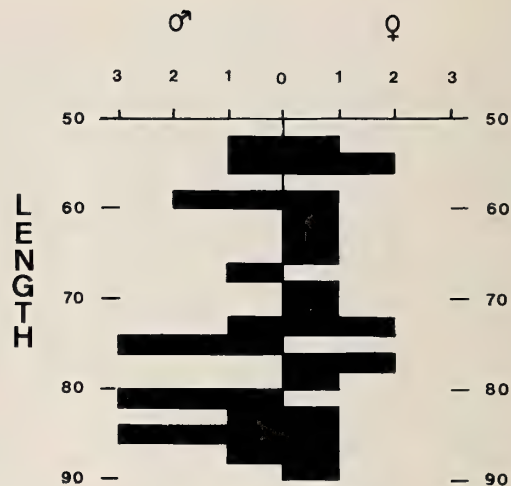


Figure 3

Size-frequency distribution of the *Aforia circinata* examined. Length in mm.

The entire gut was dissected out, placed in a Petri dish of water, and opened to determine the contents. Two of the 37 animals examined were too badly fractured to be used for shell analysis, but their gut contents were examined.

The shell shape was noted, particularly the presence or absence of a tertiary notch. Additionally, the number of major healed fractures on the anterior three whorls was determined. On some individuals, the outer aperture lip and portions of the body whorl were badly fractured during collection; hence, the number of healed fractures could not be determined. The total shell length, the width, and the aperture length were measured. If a notch was present, its height and width were measured and its position relative to the center of the major shoulder carina was determined. The width of the siphonal canal at its narrowest point was also measured (Figure 2). All measurements were made with dial calipers to 0.1 mm.

The shell measurements were transformed into their natural logarithms for the purpose of comparing measurements, for determining differences between the snail categories of large, small, males and females, and for comparing length-to-width regressions.

The pooled samples were examined by comparing (1) the natural logarithm of the shell length to the natural logarithm of the shell width, (2) the presence or absence of the notch, and (3) the variance of the ratio of natural logarithm of shell width to the natural logarithm of shell length between and within each sex. Within-sex comparisons were based on size differences, animals less than or equal to 70.0 mm being designated "small," whereas those in excess of 70.0 mm were designated large. Examination indicated sexually mature animals always exceeded 70.0 mm in shell length.

Table 1

Shell characteristics of *Aforia circinata*. / = Shell fractured; thus, the number of healed fractures is undetermined.

Shell measurements (mm)			Healed fractures			
Length	Width	Aperture length	Tertiary notch	Body whorl	Mean number per whorl	
Females						
53.1	20.0	31.2	—	/	/	
54.2	20.3	31.2	—	/	/	
54.9	20.4	34.0	—	8	4.0	
58.4	23.3	35.2	—	/	/	
61.9	23.5	33.6	ridge	/	/	
63.1	23.1	38.3	—	/	/	
64.6	23.9	37.4	—	6	2.6	
69.1	26.3	40.5	—	8	4.3	
71.5	26.7	36.0	—	3	2.0	
72.3	25.8	43.9	ridge	4	3.3	
72.5	28.0	42.4	ridge	/	/	
76.2	30.9	40.4	+	4	2.3	
77.5	28.0	42.4	+	/	/	
78.5	28.9	46.2	+	4	1.6	
82.3	30.1	48.7	ridge	6	2.6	
85.2	32.0	50.6	+	5	4.0	
87.7	32.4	54.6	ridge	3	2.3	
88.2	31.2	49.4	+	3	2.6	
			Mean:	4.9 ± 1.9	2.9 ± 0.9	(N = 11)
Males						
52.6	18.6	32.9	—	/	/	
54.7	22.5	30.6	—	/	/	
58.6	21.4	35.0	—	/	/	
59.3	22.6	27.6	—	0	1.0	
66.0	23.1	37.5	—	3	3.3	
72.3	26.0	44.1	—	4	2.0	
74.1	27.8	43.4	—	4	3.0	
75.6	27.3	43.4	—	/	/	
75.8	26.8	46.8	—	4	3.0	
80.2	26.9	45.0	—	3	1.6	
80.5	26.9	26.9	ridge	2	1.3	
81.8	31.9	50.2	—	8	4.6	
82.2	31.8	50.1	ridge	2	1.6	
84.3	30.4	49.0	—	5	2.0	
85.4	35.7	52.4	—	/	/	
85.7	32.7	51.2	—	2	1.6	
86.0	32.1	49.5	—	/	/	
			Mean:	3.4 ± 2.1	2.3 ± 1.1	(N = 11)

RESULTS

The results are unambiguous: no males have a pronounced notch, and no females smaller than 70 mm have one. All of the females that had notches were sexually mature (Table 1). Not all females have the pronounced notch, but all over 70 mm in length have either the notch or a distinct low ridge. On most of those animals with the notch, the ridge can be demonstrated at younger positions on the body whorl. Some males have a similar low ridge, albeit not as pronounced as the ridge in females. Typically, the notch arises abruptly from the ridge when the

animal is about 76 mm long, and generally does not become more pronounced as the animal gets older. The notch is a hollow fold in the outer lip and is substantially smaller in all dimensions than the siphonal canal, which it superficially resembles (Table 2). Some males have a low ridge similar to the low ridge found on the smaller females, albeit not as pronounced (Figure 1).

The allometric relationship of shell width to shell shape for all *Aforia* was $\ln W = 0.98 \ln L - 0.92$. The transformed length-versus-width relationships were fitted by linear regressions and, with the exception of small males, no significant differences were found between the allo-

Table 2

Characteristics of the tertiary notch. All measurements in mm. * = Males; all others females.

Distance from shoulder carina	Tertiary notch		Siphonal canal	Shell length when notch first evident	
	Width	Height	Width		
17.1		low ridge	4.39	70.3	
16.3		low ridge	5.82	72.3*	
18.9	1.52		4.16	74.2	
17.2		low ridge	4.96	74.8	
19.6	3.97		5.68	76.4	
19.3	1.76		4.62	77.4	
16.1	2.64		5.47	80.0	
14.0		low ridge	5.54	80.0*	
18.8		low ridge	5.82	82.0	
13.8		low ridge	3.93	fractured	
17.7		low ridge	5.17	fractured	
20.9	3.16		fractured	fractured	
Mean values (± 1 SD)					
\bar{X} :	17.5 \pm 2.2	2.61 \pm 1.01	3.73 \pm 0.88	5.05 \pm 0.68	76.4 \pm 3.9
N:	12	5	5	11	9

metric relationships of length to width between any of the subgroups. The large variance in the shell length-to-width ratio and the small sample size of the immature male group casts some doubt on the real significance of the difference. ANOVA on the \ln width/ \ln length ratio revealed significant differences between large and small animals caused by the large variances within the group of small males examined.

Healed major shell fractures (determined as shell fractures after which the pattern of spiral sculpture was altered) were common in these animals, but were not significantly more numerous in one sex. The body whorl often has more healed shell fractures than either of the next two posterior whorls (Table 1); however, this is probably a function of the relative size of the body whorl. Per unit area of shell surface, no trend is apparent.

The size-frequency distribution of these pooled samples indicates no apparent differences in the male and female components. Neither sex predominates in either the large or the small size ranges (Figure 3).

No identifiable gut contents were seen in any of the specimens; in two cases, however, sand was in the hindgut.

DISCUSSION

The hypothesis that the notch is randomly distributed throughout the species is clearly disproven. The tertiary notch of *Aforia circinata* is pronounced only in mature females. Those adult females lacking a pronounced notch have a distinct ridge, lacking in most males.

The function of the tertiary notch remains unknown, although its predominance in females suggests a possible copulatory or oviposition role. MACNIEL (1960) suggested the presence of a similar notch in the deep-water turrid

Pinguicemula might be correlated with oxygen lack and thus might function as a secondary siphonal canal. In *Aforia*, the notch may similarly function as a subsidiary canal allowing the female to shift siphonal position to ensure an adequate flow of oxygenated water while ovipositing the tough egg capsule characteristic of turrids. POWELL (1964, 1969) dismissed MacNiel's suggestion based on the callus-filled nature of some of the notches found in the deep-water tropical turrids, a condition absent in *Aforia*. If the function hypothesized here is correct, the notch might be expected in species from habitats where environmental conditions would select for accessory structures to facilitate increased oxygen flow during oviposition. POWELL (1964, 1969) stated similar notches are found in a few individuals of some deep-water tropical turrids: *Ptychosyrinx*, *Epidrella*, and *Gemmula hombroni* (Hedley, 1922). As *Aforia* is also from deep water, perhaps the notches form a common solution to some problem inherent in oviposition or copulation in deep-water habitats.

Both sexes have a large number of healed shell fractures, indicating unsuccessful attempts by shell fracturing predators, presumably crabs. There was no significant difference in the number of healed shell fractures between the sexes, and the relatively even sex ratio further argues for no differential predation. *Paralithodes camtschatica* (Tilesius, 1815), *Chionecetes opilio* O. Fabricius, and *C. bairdi* Rathbun, 1893, are found nearby in large numbers. *Paralithodes*, the Alaskan King Crab, probably has the ability to attack and break the shells of *Aforia*, although it has not been demonstrated to do so.

Aforia has a long and relatively well-documented fossil record (JAVIDPOUR, 1973). Similar low ridges are seen on illustrations of several of the fossil species illustrated by JAVIDPOUR (1973): *Aforia addicotti* Javidpour, 1973; *A.*

campbelli Durham, 1944; *A. clallamensis* (Weaver, 1916) and *A. tricarinata* Addicott, 1966. Indeed, one species, *A. tricarinata*, appears to be distinguished by the presence of just such a ridge, along with two shoulder carina. The specimens of *A. addicotti* and *A. clallamensis* figured by JAVIDPOUR (1973; figs. 12, 13) are particularly similar to *A. circinata* (Figure 1). It is unclear whether specimens without the ridge were collected in the same formations. If so, the sexual nature of the ridge, and subsequent notch, casts doubt upon the validity of these species in particular, and other species of *Aforia* described using a secondary sub-shoulder ridge as a primary characteristic.

A thorough examination of collections containing turrids from the appropriate habitats should determine how widespread the phenomenon of a tertiary notch is. If this rather peculiar shape is recognized as a normal sexual variant of shell shape and reported, then not only will data on sexual ratios of mature populations become available, but an estimate of the adaptive plasticity of the shell morphology could be obtained.

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Distribution and Radular Morphology of Various Nudibranchs (Gastropoda: Opisthobranchia) from the Gulf of California, Mexico

by

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Abstract. We report new distribution records for 14 species of nudibranchs from the tropical eastern Pacific faunal region. We present scanning electron micrographs of the radulae of *Chromodoris annulata*, *Histiomena convolvula*, and *Flabellina cynara*, and document the gorgonian prey of *H. convolvula*.

DURING THE PAST five years, we have made numerous scuba diving research trips throughout the Gulf of California. We have found specimens of opisthobranchs that constitute significant new distributional records for the tropical eastern Pacific faunal region (Panamic province).

In this paper we report new range records of 14 species of nudibranchs, present scanning electron micrographs of the radulae of three species, and document the prey of the arminid *Histiomena convolvula*. We carefully distinguish disjunct occurrences: that is, species reported from different zoogeographical marine faunal provinces that have large gaps in their known distributional ranges.

The latitude and longitude of our collecting localities are given in Table 1, and their locations are indicated on the map (Figure 16).

DORIDOIDA

PHANEROBRANCHIA

GONIODORIDIDAE

Trapania sp.

This specimen resembles the southern Californian *Trapania velox* (Cockerell, 1901). However, its color pattern

is distinct enough to warrant not immediately identifying this single specimen to the species level.

The body is white (Figures 1 and 2), with distinct chocolate-brown streaks and patches. These markings are very pronounced, clear, and sharply margined. The tips of the cephalic tentacles, rhinophores, gills, and lateral extra-branchial appendages, and the posterior extreme of the foot are a brilliant yellow.

(1) 1 specimen (20.2 mm long), subtidal, 4.5 m deep, Cabo San Lucas, Baja California Sur; leg. Alex Kerstitch (AK), 20 July 1981.

Specimens of this species have recently been reported from Isla Cedros and Bahía Vizcaino (BEHRENS, 1983).

CRYPTOBRANCHIA

CHROMODORIDIDAE

Chromodoris annulata Eliot, 1904

Known collecting records of *Chromodoris annulata* have been confined to the western Indian Ocean: from the Red Sea (GOHAR & ABOUL-ELA, 1957; ABOUL-ELA, 1959); Diani, Kenya (RUDMAN, 1973:189-190); Zanzibar and Dar es Salaam, Tanzania (ELIOT, 1904:389-390; EDMUNDS, 1971:371-372); and Natal, South Africa (BARNARD, 1927).

The following specimen represents the first collecting

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Table 1

Latitude and longitude of Mexican collecting localities.

Pacific coast of Baja California	
Islas Coronados, B.C.	32°25'N; 117°15'W
Ensenada, B.C.	31°51'N; 116°38'W
Isla San Martin, B.C.	30°31'N; 116°10'W
Bahia San Quintin, B.C.	30°24'N; 115°53'W
Isla Guadalupe, B.C.	29°00'N; 118°20'W
El Tomatal, B.C.	28°29'N; 114°04'W
Isla San Benitos	28°20'N; 115°40'W
Isla Cedros	28°07'N; 115°11'W
Bahía Vizcaino	27°50'N; 114°51'W
Punta Santo Domingo, B.C.S.	26°19'N; 112°40'W
Gulf of California, western shore	
Consag Rock, B.C.	31°07'N; 114°29'W
San Felipe, B.C.	31°01'N; 114°49'W
Puertecitos, B.C.	30°21'N; 114°38'W
Bahía de los Angeles, B.C.	28°57'N; 113°31'W
Isla Tortuga, B.C.	27°27'N; 111°58'W
Loreto, B.C.S.	26°01'N; 111°20'W
La Paz, B.C.S.	24°13'N; 110°25'W
Bahía Las Cruces, B.C.S.	24°13'N; 110°05'W
Cabo San Lucas, B.C.S.	22°52'N; 109°55'W
Gulf of California, eastern shore	
Puerto Peñasco, Sonora	31°18'N; 113°32'W
Bahía Kino, Sonora	28°49'N; 111°59'W
Morro Colorado, Sonora	27°58'N; 111°22'W
Bahía San Carlos, Sonora	27°56'N; 111°08'W
Guaymas, Sonora	27°55'N; 110°54'W
Mazatlan, Sinaloa	23°11'N; 106°25'W
Pacific coast of mainland Mexico	
Sayulita, Nayarit	21°20'N; 105°15'W
Melaque, Jalisco	19°12'N; 104°43'W
Santiago Bay, Colima	19°03'N; 104°19'W

data of *Chromodoris annulata* from the eastern Pacific Ocean, and from anywhere outside the Indian Ocean:

(1) 1 specimen, subtidal, 9 m, Isla Tortuga, Baja California; *leg.* AK, 4 April 1980.

Identification of this distinctive species is unmistakable: white body with yellow spots, dark purple margin around the mantle, and a dark purple ring around the gills with another dark purple ring enclosing both rhinophores (Figure 3).

Morphology of the radula (Figures 4 to 7) further confirms the identification. The drawings of EDMUNDS (1971: 317, fig. 15E) are nearly identical with the tooth shapes of our specimen from the Gulf of California. The small denticles are located on the lateral outer sides of each tooth, with a shift in position to the posterior surface of the outermost teeth. The present specimen had a radular formula of 56–58 (45–49.1.45–49). The combined radular formula of the 5 known specimens is: 58–75 (42–59.1.42–59). Table 2 gives the numbers of tooth rows and teeth per half-row for all these specimens. The meristic

Table 2

Meristic variation in the radula of *Chromodoris annulata*.

Rows	Maximum teeth/half-row
58	49
65	59
66	49
70	45
75	42

variations fall within the acceptable range of intraspecific variation seen in dorid nudibranchs (BERTSCH, 1976a).

This is a significant addition to the tropical west American faunal province. Further research is needed to determine whether this species is actually a more common member of the faunal province than the single collecting record would indicate. It would then show a wider distribution pattern, similar to other opisthobranch species reported to occur in this region originally based on just one specimen, such as *Dolabrifer dolabrifer* (Rang, 1828) (reported by BERTSCH, 1970), *Berghia major* (Eliot, 1903) (reported by FARMER, 1966), and *Spurilla alba* (Risbec, 1928) (reported by SPHON, 1971).

Chromodoris galexorum Bertsch, 1978 (a)

This brightly colored nudibranch, with yellow borders encircling its large red spots, is known from the central and southern Gulf of California: from Bahía de los Angeles (GOTSHALL, 1982:94) to La Paz, Baja California Sur, and from Guaymas, Sonora, and nearby islands (BERTSCH, 1978a).

The following record documents its more northerly occurrence outside the Gulf of California at an offshore island along the Pacific coast of Baja California. It may well represent an extra-limital thermally anomalous "range extension" (ZINSMEISTER, 1974). The long period of elevated water temperatures caused by an El Niño phenomenon in the eastern Pacific (personal observations; HALPERN *et al.*, 1983) may explain the presence of this tropical species at the periphery of the warm temperate California faunal province.

(1) 1 specimen, subtidal, 13.7 m, Old Sealing Station, on lee side of Isla Guadalupe, Baja California; *leg.* Jim Gatewood and Patricia S. Mariano, 22 August 1983.

Chromodoris sphoni (Marcus, 1971)

The known distribution of the red-cross colored nudibranch, *Chromodoris sphoni*, is along the mainland Pacific coast of Mexico and Central America, from Mazatlan, Sinaloa, Mexico, to Panama Bay, Panama (BERTSCH, 1978a:321). The following specimens represent its first report from inside the Gulf of California, and a northward range extension of over 670 km:

(1) 1 specimen (17 mm long), subtidal, 18 m, Isla Santa Catalina, Sonora (near Guaymas); *leg.* AK, June 1978.

(2) Approximately 30 specimens, subtidal, 12–18 m



1



2



3



4



5



6

Explanations for Figures 1 to 6

Figures 1 and 2. *Trapania* sp. collected at Cabo San Lucas. Photographs by AK.

Figure 3. *Chromodoris annulata* collected at Isla Tortuga. Photograph by AK.

Figures 4 to 6. Scanning electron micrographs of the radula of *Chromodoris annulata*. Fig. 4, 111 \times ; Fig. 5, 89 \times ; Fig. 6, 222 \times . SEMs by HB.

deep, along the Sonora coast from Morro Colorado to Bahía San Carlos; observed by AK, April–July, 1980–1982.

Mexichromis antonii (Bertsch, 1976) (b)

This relatively rare chromodorid is known from various scattered locations in the tropical west American faunal province: 3 sites on the Baja California coastline (or nearby islands) of the western Gulf of California; from the Pacific southwest coast of Mexico (Santiago Bay, near Manzanillo, Colima) and from the Pacific coast of Costa Rica (BERTSCH, 1978b:80–82). These additional records are the first reports of the species from the state of Sonora, Mexico, and from the eastern side of the Gulf of California:

(1) 2 specimens (10 and 15 mm long), subtidal, 18 m, Isla Santa Catalina, Sonora; *leg.* AK, June 1978.

(2) 30–40 specimens, subtidal, 12–18 m, along the Sonora coastline between Morro Colorado and Bahía San Carlos; seen by AK, April–July, 1980–1982.

POROSTOMATA

DENDRODORIDIDAE

Doriopsilla rowena Marcus & Marcus, 1967

This small porostome has been collected in the northern Gulf of California from the states of Sonora and Baja California: Puerto Peñasco (MARCUS & MARCUS, 1967: 205), Guaymas, San Felipe (KEEN, 1971:830), and Bahía de los Angeles (POORMAN & POORMAN, 1978:373). This represents the first report of *Doriopsilla rowena* from the state of Sinaloa and from the southern extreme of the Gulf of California; moreover it is a southern range extension of about 680 km.

(1) 1 specimen (8 mm long), Mazatlan, Sinaloa; *leg.* Antonio J. Ferreira, March 1971.

DENDRONOTOIDA

BORNELLIDAE

Bornella sarape Bertsch, 1980

This dendronotid is known to occur on both sides of the southern part of the Gulf of California, at Bahía Carisalito (4 km north of Bahía Las Cruces), Baja California Sur, and at Sayulita, Nayarit (BERTSCH, 1980). The following data extend its known range 400 km north into the central Gulf of California, and 200 km southward along the west coast of Mexico:

(1) 6 specimens, intertidal, Bahía San Carlos, Sonora; *leg.* Roy and Forrest Poorman, December 1976.

(2) 1 specimen, intertidal, Melaque, north end of Bahía de Navidad, Jalisco; *leg.* F. Poorman, February 1976.

Bornella sarape is now known to occur along more than 1200 kilometers of the western coast of mainland Mexico, with one collecting locality near the southern tip of the Baja California peninsula.

TRITONIIDAE

Tritonia diomedea Bergh, 1894

The range of *Tritonia diomedea* along the Pacific coast of the Americas is extensive; it is often cited as occurring from the Aleutian Islands, Alaska, to the Bay of Panama, Panama (BEHRENS, 1980:80). However, its known distribution is disjunct, and should be more properly cited as occurring from Shumagin Bay, Aleutian Islands, Alaska (the type locality) to Punta Santo Domingo, on the outer coast of Baja California just north of Bahía Magdalena (KEEN, 1971:834). Between these locations many specimens have been reported (see MARCUS, 1961:32–33; MACFARLAND, 1966:226–243; and THOMPSON, 1971, for a summary of these data). It is also known from the Bay of Panama and from Japan (MARCUS, 1961; KEEN, 1971). Hence, the only published record of *Tritonia diomedea* in the tropical west American marine faunal province is from its far southern waters, in Panama. There is presently a gap in its known distribution between the outer coast of Baja California (where it is known from the Surian province) and Panama. The following collecting data represent the first report of this species from the Gulf of California and in the northern portion of the Panamic marine faunal province:

(1) 1 specimen, dredged from 100 m, 3 km south of Tetas de Cabra, Bahía San Carlos, Sonora; *leg.* Roy & Forrest Poorman, 1 November 1980.

(2) 1 specimen, Morro Colorado, Sonora; *leg.* AK, 27 December 1979.

Many specimens of this species (especially those collected in California and from Punta Santo Domingo and Panama Bay) have been obtained by dredging. *Tritonia diomedea* may well be more common in the Panamic province in deeper waters. The following data from shrimp trawls indicate a temporal variation in the occurrence of *T. diomedea*:

(3) Hundreds of specimens, dredged from 70 to 100 m in shrimp trawls, between Bahía Kino and Bahía San Carlos; observed by AK, December 1980 and 1981.

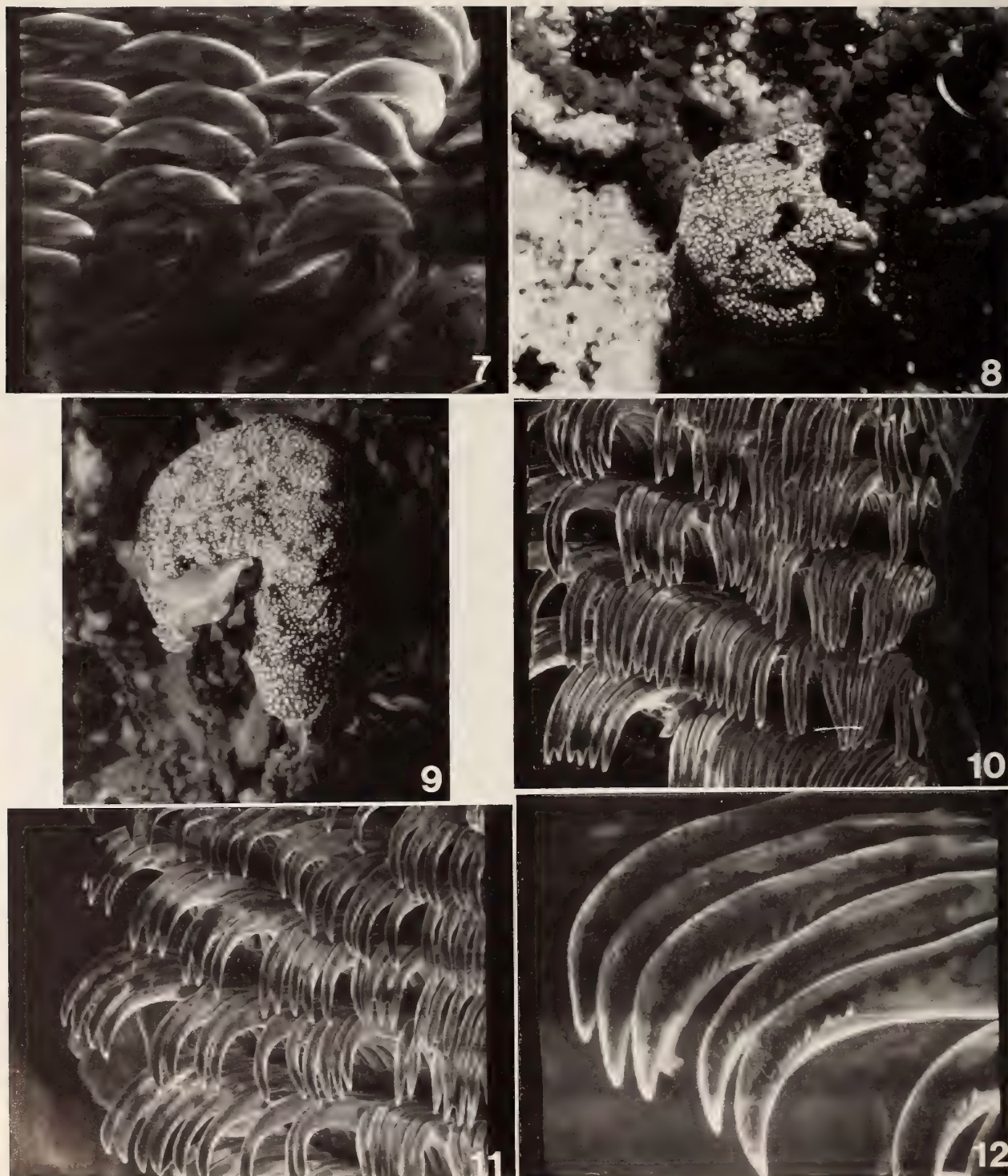
In the previous 12 years of sampling shrimp trawl material from the fishermen in this area, *Tritonia diomedea* did not appear until 1979. Not a single specimen had been observed. Since 1981 this species seems to have again disappeared from this area. During a recent trip (by AK, December 1982) not a single specimen was observed among 20 separate trawl samples.

ARMINOIDA

ARMINIDAE

Histiomena convolvula (Lance, 1962)

This rare sand-burrowing arminid has been reported from the Baja California coastline of the northern Gulf of California: Punta Diggs, 24 km south of San Felipe



Explanations for Figures 7 to 12

Figure 7. Scanning electron micrograph of the radula of *Chromodoris annulata*, 445 \times . SEM by HB.

Figures 8 and 9. In situ underwater photographs of *Histiomena convolvula* eating the gorgonian *Muricea*. Photographs by HB.

Figures 10 to 12. Scanning electron micrographs of the radula of *Histiomena convolvula*. Fig. 10, 111 \times ; Fig. 11, 111 \times ; Fig. 12, 445 \times . SEMs by HB.



Explanations for Figures 13 to 15

Scanning electron micrographs of the radula of *Flabellina cynara*. Fig. 13, 111 \times ; Fig. 14, 222 \times ; Fig. 15, 222 \times .

(LANCE, 1962), and Bahía de los Angeles (POORMAN & POORMAN, 1978:373). The following data further document the presence of *Histiomena convolvula* in Bahía de los Angeles and extend its range to the eastern Gulf of California, along the Sonora coastline:

(1) 1 specimen, subtidal, 7.6 m, NE of Punta Gringa, Bahía de los Angeles; *leg.* HB and Tom Smith, 11 December 1981.

(2) 3 specimens, subtidal, 9 m, NE of Punta Gringa, Bahía de los Angeles; *leg.* HB and David Myers, 25 January 1982.

(3) 1 specimen, subtidal, 29 m, Punta Doble, Bahía San Carlos, Sonora; *leg.* AK, 15 April 1979.

Three of the four specimens found by Bertsch, Smith, and Myers in Bahía de los Angeles were eating the gorgonian *Muricea cf. californica* (Figures 8 and 9). This is the first report of the prey of *Histiomena convolvula*. All four specimens in Bahía de los Angeles were encountered

on the deeper seaward edge of a series of rock reefs, where the bottom becomes sandy.

The radula consists of numerous hook-like teeth (Figures 10 and 11). LANCE (1962:53–54; fig. 6c) reported that some of the middle lateral teeth bear extremely fine denticles along the side of the cusp; these are clearly shown in the scanning electron micrograph (Figure 12).

AEOLIDIIDA

FLABELLINIDAE

We follow GOSLINER & GRIFFITHS (1981) in the generic placement of these two species of *Flabellina*.

Flabellina cynara (Marcus & Marcus, 1967)

This elegant eolid is known to swim by back-and-forth strokes of its whiplike cerata, bringing head and tail rhythmically together. *Flabellina cynara* has been reported



Figure 16

Map of northwestern Mexico showing collecting localities.

from various localities in the extreme northern Gulf of California: Cholla Bay, Puerto Peñasco, Sonora (MARCUS & MARCUS, 1967:220); dredged in 38 m of water off Consag Rock (FARMER, 1970:84); and dredged off Puertecitos (KEEN, 1971:836). The following records are southern range extensions of over 430 km and 210 km respectively along each side of the Gulf of California. The range of *Flabellina cynara* can now be cited as throughout the northern half of the Gulf of California.

(1) 1 specimen (45 mm long), subtidal, 12 m, Guaymas, Sonora; *leg.* AK, 28 June 1981.

(2) 1 specimen, subtidal, 15 m, S end Smith Island, Bahía de los Angeles, Baja California; *leg.* David K. Mulliner, 17 October 1979.

The triserial radula (Figures 13 to 15) had 18 rows of teeth; it was a larger specimen than the holotype which had 16 rows of teeth (MARCUS & MARCUS, 1967:221). Each central tooth bears 7–10 denticles (rather than just

the 7–9 originally reported). The scanning electron micrographs (Figures 13 to 15) show a morphological variation that was not reported in the light-microscopy-based original description. Some of the lateral teeth, “obtuse-angled triangles” (MARCUS & MARCUS, 1967:221), bear 2 rows of denticles—the large and obvious grasping denticles below the cusp on the inner surface and a row of 5 or 6 minute denticles on the outer slope of the tooth (Figures 13 and 14). As can be seen, not all teeth show this feature.

Flabellina iodinea (Cooper, 1863)

The range of *Flabellina iodinea* has been cited as Vancouver Island, British Columbia, Canada, to the Gulf of California, Mexico (BRUSCA, 1980:194), to Puerto Peñasco (BEEMAN & WILLIAMS, 1980:336–337), or to Bahía de los Angeles (FARMER, 1980:122). However, known distribution records do not exist from the southern coasts of Baja California, nor in the southern Gulf of California. Previous collecting data should have been summarized to reflect this disjunct known distribution: from Vancouver Island to Cabo San Quintín (SPHON, 1972:64; BEHRENS, 1980:92; McDONALD & NYBAKKEN, 1981:60), including the Coronados Islands (LANCE, 1961) and Ensenada (FARMER & COLLIER, 1963) in northern Baja California. This species has been reported in the Gulf of California from two locations: Puerto Peñasco (MARCUS & MARCUS, 1967:218) and Bahía de los Angeles (POORMAN & POORMAN, 1978:373; HAMANN, 1981).

The following data, therefore, are especially significant because they establish its presence at intermediate localities along the Pacific coast of Baja California, at the extreme southern tip of the peninsula, and from a second locality in the eastern Gulf of California:

(1) BEHRENS (1983) reported collecting specimens at Islas San Martin, San Benitos, and Cedros, Baja California.

(2) 3 specimens, intertidal, El Tomatal, Baja California; HB, 14 June 1983.

(3) 1 specimen, subtidal, 76 m, Cabo San Lucas, Baja California Sur; leg. AK, August 1972.

(4) Punta Doble, Bahía San Carlos, Sonora; leg. AK. various: 1 specimen, 29 m, April 1983; 1 specimen, 16.8 m, December 1978; 3 specimens, 29 m, April 1979; more than 30 specimens, subtidal, April 1982.

Flabellina iodinea occurs rarely in the Gulf of California, but usually under situations of colder water, especially in deeper subtidal waters (our records; also those of POORMAN & POORMAN, 1978, who dredged *F. iodinea* from Bahía de los Angeles; and HAMANN, 1981, who reported collecting it below the thermocline at 15 m in Bahía de los Angeles). The single specimen collected at Puerto Peñasco is an exception to this generalization. With current knowledge, we can best describe the range of *F. iodinea* as common throughout the Oregonian and Californian marine faunal provinces, from Vancouver Island, British Columbia, to Isla Cedros, Baja California; rarer in the

northern Panamic province (throughout the Gulf of California) in deeper or colder waters.

GLAUCIDAE

Glaucus atlanticus Forster, 1777

This species is a pelagic, circumtropical member of the wind-driven Portuguese man-of-war (*Physalia*) community (BERTSCH & JOHNSON, 1981:100). The toxic stinging capability of *Glaucus*, which stores the largest and most potent nematocysts of *Physalia*, is well documented (THOMPSON & BENNETT, 1969; BINGHAM & ALBERTSON, 1974).

In the eastern Pacific it has been collected off west-central America, from latitude 24°N, south to latitude 8°S (KEEN, 1971:840). These data are the first records from well inside the Gulf of California:

(1) Numerous specimens (10–20 mm), off Bahía San Carlos, among drifts of *Physalia* and *Porpita*; observed by AK, summers 1978, 1979, and 1981.

(2) Several hundred specimens (10–20 mm), off Cabo San Lucas, among drifting *Physalia* and *Porpita*; observed by AK, summers 1978, 1979, and 1981.

AEOLIDIIDAE

Baeolidia nodosa (Haefelfinger & Stamm, 1958)

This species is widely distributed in the tropical east and west Atlantic, including the Mediterranean and Caribbean Seas (HAEFELFINGER & STAMM, 1958; MARCUS & MARCUS, 1970:89; SCHMEKEL, 1972:152–159; TEMPLADO, 1981). In the central Pacific Ocean it has been reported from Oahu and Kauai, Hawaiian Islands (KAY, 1979:488; GOSLINER, 1980:66–69; BERTSCH & JOHNSON, 1981:102), and in the eastern Pacific in the Gulf of California from Bahía Las Cruces, Baja California Sur (BERTSCH, 1972:104–105).

The following record is only the second report of this species in the Gulf of California, and a northward range extension (of over 400 km) from Bahía Las Cruces to the Sonoran coast:

(1) 1 specimen, on floating *Sargassum*, off Bahía San Carlos, Sonora; leg. AK, June 1978.

Spurilla neapolitana (Delle Chiaje, 1823)

This eolid has been reported numerous times throughout the tropical Atlantic, including the Mediterranean and Caribbean Seas (cf. GOSLINER, 1980:64–65, for a summary of the literature and synonymy). Moreover, this species has been reported from the central Pacific (Oahu, Hawaiian Islands; KAY, 1979:489; GOSLINER, 1980) and the eastern Pacific (“Gulf of California”; BERTSCH, 1979:59). It thus shares a similar distribution pattern with *Baeolidia nodosa*: throughout the tropical Atlantic (and adjacent seas); Hawaii, and Gulf of California in the central and eastern Pacific. This species’ distribution is not appropriately termed “circumtropical” (KAY, 1979;

GOSLINER, 1980) since it has not yet been reported from the Indo-West Pacific.

The following data detail known collecting sites in the Gulf of California:

(1) 1 specimen (55 mm long), intertidal, Morro Colorado, Sonora; *leg.* AK, 19 December 1977 (deposited egg mass in aquarium).

(2) 1 specimen, subtidal, 9 m, off Isla San Nicholas, Bahía San Carlos, Sonora; *leg.* AK, December 1979 (laid eggs in aquarium).

(3) 3 specimens (25 mm long), intertidal, Puerto Escondido (24 km south of Loreto), Baja California Sur; *leg.* Robin Hugh Alexander Boroch and Deborah J. Kasten, 28 June 1980.

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The Diets of Alaskan *Neptunea*

by

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Abstract. Diets of *Neptunea pribiloffensis*, *N. lyrata*, *N. heros*, and *N. ventricosa* from a series of subtidal sites in the Bering Sea, and *N. lyrata* and *N. pribiloffensis* from an intertidal habitat in south-central Alaska, were examined and compared. All species were found to feed primarily upon bivalves and polychaetes, secondarily upon carrion. *Neptunea pribiloffensis*, in particular, appears to feed on live polychaetes and bivalves. Other prey taxa are well represented in the diets of these large whelks.

In the Bering Sea, these four species are found in two paired groups. *Neptunea heros* and *N. ventricosa* are the more northern, colder-water pair, and *N. pribiloffensis* and *N. lyrata* are the southern, warmer-water pair. Diets of each species within each pair are similar and the pooled diets of both species within each pair are similar when both pairs are allopatric. When all four species are sympatric, the diets overlap significantly less. Similarly, the diets of *N. lyrata* and *N. pribiloffensis* from south-central Alaska overlap substantially with the diets of all four species from the non-overlap regions of the Bering Sea, but overlap significantly less with diets of all four species from the region of sympatry.

INTRODUCTION

LARGE GASTROPODS of the family Buccinidae, often very abundant in north-temperate and boreal areas (PETERSEN, 1911a, b, 1913; BLEGVAD, 1914; NIELSEN, 1975; NAGAI & SUDA, 1976; PEREYRA *et al.*, 1976; TAYLOR, 1978; TAYLOR *et al.*, 1980), are presumed to be carrion feeders and facultative carnivores. Considering the diversity of the family (BAXTER, 1981) and the relatively large size and economic importance of the snails, however, their diets are relatively unknown (BLEGVAD, 1914; HUNT, 1925; AVERY, 1961; PEARCE & THORSON, 1967; VILLEMURE & LAMOUREUX, 1975; TAYLOR, 1978).

In the eastern Bering Sea and in south-central Alaska, the dominant marine gastropods, in size and biomass, belong to the buccinid genus *Neptunea*. *Neptunea* is circum-boreal, but has a center of distribution in the north-central Pacific-Bering Sea region (NELSON, 1978). The diet of the European *Neptunea antiqua* (Linnaeus, 1758) has been examined (PEARCE & THORSON, 1967; TAYLOR, 1978), but few feeding observations have been made for any of the Pacific species (AVERY, 1961). The four largest and most abundant species of *Neptunea* in the eastern Bering Sea are *N. lyrata* (Gmelin, 1791), *N. pribiloffensis* (Dall, 1919), *N. heros* (Gray, 1850), and *N. ventricosa* (Gmelin, 1791). Together with some other large gastropods, they

are the basis for a small pot fishery in the Bering Sea (MACINTOSH, 1978). In most Atlantic areas, however, buccinids have been considered an economic nuisance (PETERSEN, 1911b), although recently some attempts have been made to assess population sizes in anticipation of fisheries attempts (VILLEMURE & LAMOUREUX, 1975).

Information on the Bering Sea neptunes is fragmentary (PEREYRA *et al.*, 1976; MACINTOSH & PAUL, 1977); nonetheless, they are clearly an important component of that region's benthic fauna. The Bering Sea benthos consists of two major faunal assemblages, each somewhat correlated with depth, and certainly correlated with characteristic bottom-water temperatures. The low-Arctic-Boreal assemblage, found in the northwestern portions of the Bering Sea, is correlated with bottom temperatures exceeding 2°C only briefly in the summer, generally is found in depths in excess of 50 m, and contains *N. heros* and *N. ventricosa*. The Subarctic-Boreal assemblage, found in the southern and southeastern portions of the basin, exists where the bottom temperature is a relatively constant 2-4°C, is characteristic of shallow waters, and contains *N. lyrata* and *N. pribiloffensis* (NEIMAN, 1963; NAGAI & SUDA, 1976; PEREYRA *et al.*, 1976; MACINTOSH & PAUL, 1977). The replacement of one faunal assemblage by the other occurs in a transition zone often in excess of 50 km wide. With the exception of several cosmopolitan species, mainly polychaetes, most invertebrate benthic taxa are represented by different species in the two regions (NEIMAN, 1963).

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Portions of the Subarctic-Boreal assemblage are found south of the Aleutians. In particular, *N. lyrata* and *N. pribiloffensis* have ranges extending to at least the Washington coast. They appear to follow a thermal gradient, for they are characteristically deep-water species there (RICE, 1972; ABBOTT, 1974). Both species are found intertidally in south-central Alaska. In some cases, they are the most abundant gastropods in the low intertidal zone (SHIMEK, 1981).

Buccinid gastropods are presumed to be primarily scavengers or carrion feeders. This assumption is based on three premises. Firstly, they lack the accessory boring organ found in the muricid gastropods; consequently, they are unable to attack efficiently bivalve or barnacle prey by boring. Secondly, they come readily to bait. And finally, those few whose diets have been examined have been shown to eat a wide variety of prey. Based on preliminary field observations, I hypothesized that Alaskan *Neptunea* are predatory and only rarely eat carrion. I asked the following questions. What is the diet of each species? Is there any specialization with regard to either prey taxon or prey guild? Can the food be characterized as having been alive or dead? What is the overlap in the diets of sympatric species? If they are predominantly scavengers, the dietary overlaps should be higher than if they are predators, assuming some predator-prey specialization. And, in areas of geographical overlap, are the diets of the species similar?

I examined gut contents of adults and large juveniles of the four *Neptunea* species. By identifying the snails' gut contents as precisely as possible, I hoped to determine their diets. *Neptunea* is a large genus containing many similar species (GOLIKOV, 1961, 1963; NELSON, 1978), and the radulae are similar and unspecialized in the species examined (KANG, 1976; Shimek, unpublished observations). Feeding structures are often strongly correlated with the prey taken, especially in specialized carnivorous gastropods (NYBAKKEN, 1970; NYBAKKEN & McDONALD, 1981; SHIMEK, 1983a), although the adaptive significance of some of these structures remains obscure. The similarities in the radulae and the similar gut morphologies of all four *Neptunea* species examined indicate prey items are probably captured and digested similarly in these species.

MATERIALS AND METHODS

Bering Sea snails were collected using an Eastern otter trawl constructed with 10.2-cm mesh on the wings and body and 8.5-cm mesh in the intermediate section and cod-end. The cod-end was lined with 3.2-cm mesh. Few snails smaller than 50 mm in total length were collected. Furthermore, as the net's behavior on the bottom was unpredictable, the samples from different sites must be considered qualitative; however, they were assumed to be comparable. Trawl-collected animals were either preserved in 70% isopropyl alcohol or frozen. Trawl-collected

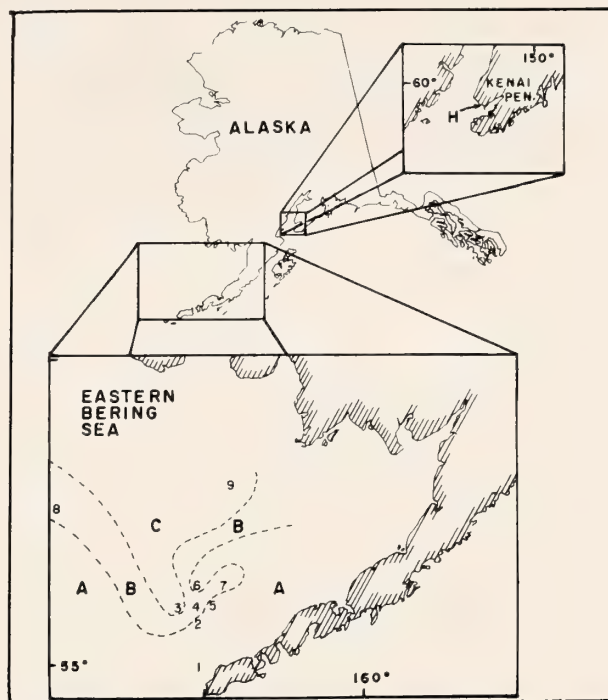


Figure 1

Map of Alaska showing snail collecting sites. A, region of *N. lyrata* and *N. pribiloffensis* pair only; B, region where all species are found; C, region of *N. heros* and *N. ventricosa* pair only; H, intertidal site near Homer, Alaska. Numbers refer to the collecting sites detailed in Table 1.

specimens came from several locations in the Bering Sea (Table 1, Figure 1).

Field observations were made on a mixed *N. lyrata*-*N. pribiloffensis* assemblage living on a low (-1.0 to -1.5 m below MLLW) intertidal sandstone bench near Homer, Alaska (59°38'N; 151°27'W), to determine feeding meth-

Table 1

Bering Sea snail collection localities.

Area	Position	Number	Number collected			
			<i>lyr.</i>	<i>prib.</i>	<i>vent.</i>	<i>heros</i>
A	54°59'N; 165°09'W	1	18			
A	55°59'N; 165°10'W	2	116	38		
A	56°39'N; 165°09'W	6	2	1		
A	56°20'N; 164°35'W	5		48		
B	56°19'N; 165°12'W	4		34	21	
B	56°39'N; 164°13'W	7	45	7	68	14
B	57°39'N; 169°39'W	8				32
C	56°20'N; 165°47'W	3			63	
C	58°00'N; 164°01'W	9			54	100

Table 2

Gut contents of *Neptunea* species. * = Some Homer *N. pribiloffensis* had more than one item in their guts.

Species:	<i>N. pribiloffensis</i>			<i>N. lyrata</i>			<i>N. heros</i>		<i>N. ventricosa</i>		TOTAL
Area:	A	B	H	A	B	H	B	C	B	C	
Contents:											
Hydrozoa								3	3		6
Polychaeta	7	14	29	14	2	3		12	1	13	95
Cirripedia				4			2	1	4	6	17
Decapoda	1				1						2
Bivalvia	9		28	26	1	7	7	8	3	21	110
Gastropoda							2				2
Ophiuroidea							1				1
Osteichthyes				1					1	1	3
Sand	14	9	23	25	3	12	5	11	3	16	121
Unidentified	3		26	6	6	5	5	16	20	9	96
TOTAL FEEDING	34	23	106 (98)*	76	13	27	22	51	35	66	453 (445)*
No contents	53	18	72	60	32	25	24	49	53	51	437
TOTAL	87	41	170	136	45	52	46	100	88	117	882

ods, and to assess the range of prey taken. Field-collected animals were frozen for later analysis. Band transects were done monthly from May through September, 1979, to assess the number of animals in each habitat.

Feeding animals were noted and their food was determined if possible. The intertidal bench was a heterogeneous area consisting of three major habitats: a silt-cov-

ered sandstone bench area, areas of cobble, and areas of dense mats of the sabellid polychaete *Schizobranhia insignis* Bush, 1904. Samples of the infauna were collected by recovering all of the sediment from 0.25-m² randomly placed quadrats in the worm-mat areas and the silt-covered inter-mat areas. Sediment collected for analysis was fixed for 24 h in 10% seawater-formalin, stained with

Table 3

Dietary overlaps of *Neptunea* species by area.

# Species—Area	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
1. <i>N. lyrata</i> —A		○	○	○	○	●	●	●	●	●
2. <i>N. pribiloffensis</i> —A	0.841		○	○	○	●	●	●	□	●
3. <i>N. pribiloffensis</i> —H	0.802	0.868		○	●	○	●	●	□	●
4. <i>N. ventricosa</i> —C	0.934	0.829	0.808		○	●	●	●	●	□
5. <i>N. lyrata</i> —H	0.922	0.829	0.791	0.812		●	●	●	□	□
6. <i>N. heros</i> —C	0.686	0.745	0.833	0.692	0.633		●	□	●	●
7. <i>N. lyrata</i> —B	0.561	0.721	0.750	0.567	0.550	0.750		□	□	●
8. <i>N. heros</i> —B	0.667	0.529	0.491	0.659	0.583	0.333	0.250		●	■
9. <i>N. ventricosa</i> —B	0.400	0.333	0.333	0.504	0.333	0.438	0.333	0.417		■
10. <i>N. pribiloffensis</i> —B	0.500	0.412	0.509	0.317	0.300	0.500	0.500	0.000	0.083	

Mean + 1 SD < D < Mean + 2 SD = 0.795–1.000 indicated by: ○

Mean D = 0.570 ± 0.224 Mean – 1 SD ≤ D ≤ Mean + 1 SD = 0.346–0.794 indicated by: ●

Mean – 2 SD < D < Mean – 1 SD = 0.121–0.345 indicated by: □

D < Mean – 2 SD = 0.000–0.120 indicated by: ■

 $H_0: D_{Bi} > D_{jk}$ where $i = A, B, C, H$; and where $j, k = A, C, H$.Mean $D_{Bi} = 0.454 \pm 0.177$ N = 30Mean $D_{jk} = 0.802 \pm 0.084$ N = 15Calculated $t = 7.18$, 43 d.f. $t_{0.001, 60} = 3.460$; therefore reject H_0 with $\alpha < 0.001$

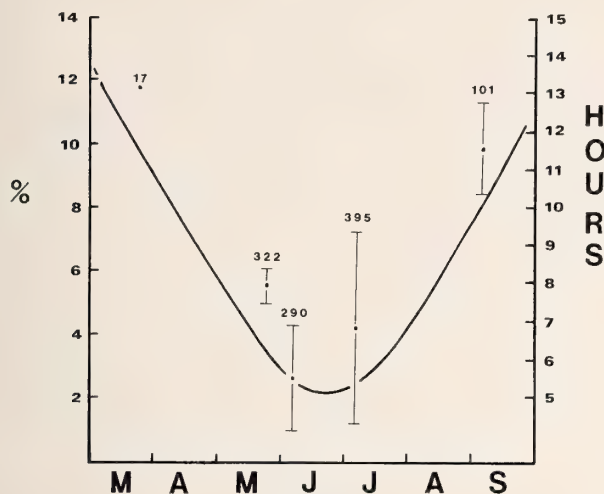


Figure 2

Relationship between percent of animals observed feeding (mean \pm 1 SD) and the number of hours between sunset and dawn. Left ordinate gives percent feeding (●), where numbers indicate the number of snails examined during a given sampling period. Right ordinate gives hours between sunset and sunrise at this latitude (indicated by the solid line). Spearman Rank Correlation Coefficient between observed feeding percentage and sunset-sunrise time = 1.

Rose Bengal, and stored in 70% isopropyl alcohol. The sediment was sieved through 0.5-mm screens and animals retained on the screens were identified. Polychaetes and bivalves, potential prey, were identified to species; other taxa were generally identified to class.

Snails returned to the laboratory were removed from the shell, sexed, and the stomach and hindgut were examined for contents. Preliminary examination of the mouth and esophagus in 150 animals yielded no contents; thus, examination of the foregut was not done for the majority of the specimens. Gut contents were examined microscopically and identified if possible, using standard references. Results were analyzed using *t*-tests, and log-likelihood ratios (SOKAL & ROHLF, 1969). Similarity in diets was compared using the common lowest percentage or "D" index (SCHOENER, 1968).

RESULTS

Gut contents of 128 *N. lyrata*, 181 *N. pribiloffensis*, 146 *N. heros*, and 205 *N. ventricosa* from the eastern Bering Sea were analyzed by area. Similarly, the gut contents of 52 *N. lyrata* and 170 *N. pribiloffensis* from the Homer area were examined (Table 2).

About half of the animals examined had empty guts. The others contained a wide variety of items, but generally the most abundant recognizable items were bivalve fragments (ctenidial remains, shell fragments, or cuticular siphonal coverings), polychaete remains (fragments with

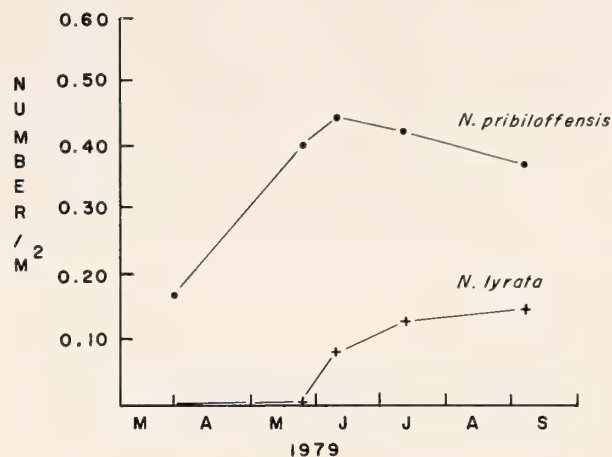


Figure 3

Observed abundance of *Neptunea* spp. at site H.

setae or whole worms), or barnacles (trabeculate plates, cirri, or entire animals except for the calcareous plates).

A large fraction of the contents consisted of sand and unidentifiable tissue fragments. These categories were excluded from the dietary overlap analyses. The absolute and relative frequencies of these categories varied from species to species, and within species from area to area.

Dietary overlap analyses were done using only the identifiable gut contents. To ensure consistency of interpretation, the general systematic category utilized was class (Table 2). Bering Sea snails exhibited substantial differences in diet within a species between areas of non-overlap (Areas A, C) and overlap (Area B, Table 3). *Neptunea lyrata* and *N. pribiloffensis* diets within area A overlap substantially, as do the diets of *N. heros* and *N. ventricosa* within area C. Furthermore, these two pairs of species have diets that overlap to a high degree (Table 3). The diets from area B are much less similar. There is a general trend for any species' diet in the overlap area to be different from its diet in either area A or C. There is also high overlap between the diets of *N. lyrata* and *N. pribiloffensis* from the Homer area, and these diets are similar to the diets of the respective species from area A. The mean dietary overlap for all species combinations between and within areas A, C, and H is significantly higher than the mean dietary overlap for all species combinations between areas A and B, C and B, H and B, and all species combinations within area B (Table 3).

Field observations of feeding at Homer generally confirm the diet as consisting of either polychaetes or bivalves, although the fraction of snails feeding is very low compared to the fraction with food in their guts (Table 4). The number and fraction of *N. pribiloffensis* observed feeding varied monthly, and were highly correlated with the amount of time between sunset and sunrise, indicating that feeding is largely nocturnal, at least intertidally (Figure 2).

Table 4

Frequency of dietary items. * = More than one food item per snail for some categories.

Species: Area:	Gut contents										Field feeding observations	
	<i>N. pribiloffensis</i>			<i>N. lyrata</i>			<i>N. heros</i>		<i>N. ventricosa</i>		<i>N. pribiloffensis</i>	<i>N. lyrata</i>
	A	B	H	A	B	H	B	C	B	C		
Contents:												
Hydrozoa								0.03	0.03			
Polychaeta	0.08	0.34	0.18	0.10	0.18	0.06		0.12	0.01	0.11	0.02	0.01
Cirripedia				0.01			0.04		0.03	0.05		
Decapoda	0.01				0.02						<0.01	
Bivalvia	0.10		0.16	0.21	0.02	0.13	0.15	0.08	0.03	0.17	0.02	0.03
Gastropoda							0.04					
Ophiuroidea							0.02					
Osteichthyes				0.01					0.01	0.01		
Sand	0.16	0.22	0.14	0.18	0.07	0.23	0.11	0.11	0.03	0.14		
Unidentified	0.03		0.15	0.04	0.13	0.10	0.11	0.16	0.23	0.08		
Nothing	0.61	0.44	0.42	0.44	0.71	0.48	0.52	0.49	0.60	0.44	0.95	0.97
TOTAL	0.99	1.00	1.05*	0.99	0.99	1.00	0.99	0.99	0.97	1.00	0.99	1.01
Number	87	41	170	136	45	52	46	100	88	117	1125	185

Estimates of prey availability are not present for the Bering Sea populations, but are available for the intertidal population (Table 5). The sabellid *Schizobranchia insignis*, the relatively large rock-burrowing bivalve *Zirfaea pilsbryi* Lowe, 1931, and polychaetes in general are abundant.

Carion suitable for scavengers was seen occasionally, but was too rare for quantitative abundance estimates to be meaningful. Both species of *Neptunea* were relatively abundant in this intertidal area (Figure 3).

Only within the Polychaeta was prey discrimination to

Table 5

Infaunal organisms at Homer area.

Taxon	Mean number per m ² ± 1 SD			
	May		September	
	Worm mat	Bare bench	Worm mat	Bare bench
Cnidaria		525 ± 742		3175 ± 601
Phoronida		20 ± 6		8 ± 11
Priapulida		8 ± 11		
Annelida				
Oligochaeta	18,800 ± 3191	2019 ± 547	20,000 ± 20,365	1050 ± 212
Polychaeta				
Maldanidae	6756 ± 470	16 ± 23	5350 ± 1061	125 ± 106
Nephtyidae	40 ± 11	31 ± 1	400 ± 424	
Nereidae	46 ± 3	600 ± 34	650 ± 261	220 ± 28
Pectinariidae			900 ± 849	
Polynoidae	230 ± 14	367 ± 58	200 ± 282	
Sabellidae	41,598 ± 1536	15,385 ± 5071	16,250 ± 1060	50 ± 72
Others	7677 ± 1747	15,385 ± 4606	23,050 ± 1095	83,320 ± 45,368
Mollusca				
Bivalvia				
<i>Zirfaea pilsbryi</i>	22 ± 19	23 ± 37	22 ± 35	20 ± 24
Others	3893 ± 1121	600 ± 237	10,300 ± 1229	1678 ± 2011
Gastropoda	186 ± 32	238 ± 274		
Arthropoda	3406 ± 1491	13,270 ± 4624	15,300 ± 6075	11,050 ± 1485
Echinodermata			50 ± 71	
TOTAL	86,654 ± 13,448	48,448 ± 6856	94,472 ± 16,663	100,621 ± 20,743

Table 6
Polychaete prey of *Neptunea*.

Species:	<i>N. pribiloffensis</i>			<i>N. lyrata</i>			<i>N. heros</i>		<i>N. ventricosa</i>		TOTAL
Area:	H	A	B	H	A	B	B	C	B	C	
Family:											
Spionidae	2									1	3
Cirratulidae			2		3			8		6	19
Maldanidae	1	1	9	1	2					1	15
Polynoidae				1							1
Nereidae	2										2
Nephtyidae	3										3
Sabelliidae	2										2
Pectinariidae	1										1
Ampharetidae								2			2
Terebellidae		3			1			1		1	6
Sabellidae	20		1	1	2					3	27
Unidentified	0	2	2	0	6	2	0	12	1	13	39
TOTAL	31	7	14	3	14	2	0	23	1	25	120

a systematic category lower than class possible. Polychaete remains were generally identifiable to family and occasionally to species, although the lack of specimens for confirmational comparison of setal morphologies from the Bering Sea areas makes the latter identifications somewhat doubtful. Some similarity is seen in the polychaete prey taken when considered area by area (Table 6). Errant polychaetes, absent from the guts of the Bering Sea snails, were commonly found in the guts from the Homer *N. pribiloffensis*. Maldanids seemed to be a favored food for *N. lyrata* and *N. pribiloffensis*, whereas cirratulids were taken more frequently by *N. heros* and *N. ventricosa*.

DISCUSSION

The large *Neptunea* species of the eastern Bering Sea and south-central Alaska are clearly divisible into two groups of species pairs of similar dietary and habitat utilizations. When the two groups are allopatric, the northern, colder-water pair, *N. heros* and *N. ventricosa*, has a high dietary overlap with the southern group, *N. lyrata* and *N. pribiloffensis*. The benthic fauna in the Bering Sea is characterized by a few widely spread assemblages and a larger number of smaller, more local ones (NEIMAN, 1963). Replacement of one major assemblage by another is gradual, and is often accomplished by the replacement of one species by another similar species (i.e., *N. heros* by *N. lyrata*; *N. ventricosa* by *N. pribiloffensis*) rather than by wholesale changes in the character of the fauna (NEIMAN, 1963). Quantitative data for changes in the infauna in this region are not available, but given the noted gradual changes in the epifauna (PEREYRA *et al.*, 1976) and similar qualitative observations about the infauna (NEIMAN, 1963), it is reasonable to infer that the composition of the infauna at the class level is relatively consistent.

The dietary similarity between the Homer and Bering

Sea populations of the *N. lyrata*-*N. pribiloffensis* group strengthens the argument that this pair of species chooses similar prey categories wherever it is found. The two habitats are strikingly different; the Homer area is a rocky sandstone beach, whereas the Bering Sea area A is a relatively flat sandy subtidal plain, yet the diets show a high degree of overlap at the class level.

If scavenging is defined as eating carrion, then tubicolous polychaetes and bivalves are unlikely items to be represented in the diets of scavengers. Both prey types bury in the substrate and upon death are immediately covered by sediment. *Neptunea* could be scavenging food, however, from the remains of some other organisms' meals. The presence of entire polychaetes and barnacles, and, effectively, the remains of entire gastropods (no shell; the remains were macerated, but substantially complete) argue against this. Furthermore, field feeding observations indicated *N. pribiloffensis* and *N. lyrata* can easily eat large bivalves that cannot close their shells completely.

The piddock *Zirfaea pilsbryi* is commonly found burrowed into the sandstone of the Homer area. Both *Neptunea* species feed on it by extending their proboscides down the siphon and rasping away the flesh of the body. A specimen of *Neptunea pribiloffensis* with a shell length of 40 mm can extend its proboscis over 35 cm, allowing easy feeding on buried infauna. In the Bering Sea samples, many of the bivalve remains contained rolled masses of cuticle, which when unrolled were obviously the cuticular coverings from clam siphons similar to the siphons of *Mya*. *Mya* species gape; and *Mya truncata*, a common arctic bivalve, is present in the Bering Sea (NEIMAN, 1963; ABBOTT, 1974).

In the Homer area, many individuals of *N. pribiloffensis* were seen feeding similarly on the sabellid polychaete *Schizobranchia insignis*. They would extend their proboscides into the polychaete tubes and eat the worms. The

worms are gregarious and their tubes often tightly intertwine. It is likely that worms adjacent to the one whose tube was initially penetrated also are eaten. As many as five specimens of *S. insignis* were found in the gut of one *N. pribiloffensis*. Other polychaetes were taken by *N. pribiloffensis*, and these prey do not appear to be randomly selected, as some taxa eaten are rare in the sediment samples. The significance of these choices remains unclear. *Neptunea pribiloffensis* is clearly adept at capturing errant as well as tubicolous sedentary worms, indicating that this species in particular can be a predator on mobile prey.

The analysis of the polychaete prey also shows that the similarities seen in diets are to some extent an artifact of the analysis. Within the class Polychaeta, the prey taken are distributed among 11 families and probably more than 20 species. Thus, although these whelks form a predatory guild adapted to exploiting polychaetes and bivalves, it is unlikely that they are in direct competition with one another for any one species of prey.

Bivalves have been shown to be important dietary components in these (present study) and other *Neptunea* (BLEGVAD, 1914; PEARCE & THORSON, 1967; TAYLOR, 1978), and I suspect both the sand and unidentified tissue remains to be primarily the result of consuming bivalves. Bivalve tissues have few overt structural clues as to taxonomic origin and, thus, are difficult to identify when partially digested. The dense sand probably passes through the guts of *Neptunea* slower than most tissue fragments, resulting in some specimens containing only sand in their guts. In many specimens, gut contents clearly identifiable as being of bivalve origin contained a large fraction of sand in the midgut and unidentifiable tissue fragments in the hindgut. In most cases then, the categories of sand and unidentifiable tissue fragments probably represent the remains of deposit-feeding bivalves, or bivalves that inadvertently ingested sediment. Items clearly dead when eaten were a small constant dietary fraction for all four species. These items included fish remains (scales and tissue), king crab (*Paralithodes* sp.) remains (a dactyl), and a complete pandalid shrimp molt. The ophiuroid remains collected in one *N. heros* included only fragments of one ray, and may indicate scavenging. In the intertidal area, no *N. lyrata* and only one of 1125 *N. pribiloffensis* were observed eating carrion, a small dead *Cancer magister*.

CONCLUSIONS

Neptuneid gastropods must be considered to be primarily predators on live prey, not scavengers or carrion feeders. This conclusion is supported by the predominance of live food in the diet and the dietary shift seen in the overlap zone. The distribution of carrion should be relatively independent if viewed at the class level, providing the faunal assemblages are generally comparable. The array of utilized prey is less diverse than the array of potential prey in the Homer area, indicating specialization on the described prey. The dietary shifts would be expected when

two food-limited systems overlapped, as each competing species pair was forced to utilize a more diverse, but less desirable suite of food, although it is unlikely that direct competition exists for any one prey species.

These four species exist as two paired species guilds adapted for exploitation of deeply dwelling or large infauna, although they are not bound to the resource. The extremely long proboscides of these snails are probably the major structural adaptations allowing exploitation of the large bivalves and tubicolous polychaetes as major resources. The snails are morphologically very similar and the diets within each guild are also quite similar. They are, however, reproductively isolated; each species has distinctly different egg capsules (GOLIKOV, 1963; SHIMEK, 1981). Predation on boreal soft-sediment infauna is uncommon among large prosobranchs. The naticids appear to be the only other successful group of large snails to exploit this resource. Because of their ability to bore shells, the naticids are apparently specialists on mollusks. The neptuneids exploit a wider array of potential prey, including polychaetes and cirripedes. In most soft-sediment communities, polychaetes are a major constituent in terms of species number, absolute number, and biomass. The polychaetes harvested by these *Neptunea* are large, although the juveniles probably take smaller worms.

Soft-sediment vermivory is best exemplified in prosobranchs by the immensely large and successful family Turridae (SHIMEK & KOHN, 1981; SHIMEK, 1983a, b, c), but the turrids in the north-central and north-eastern Pacific are generally small. These small snails, primarily in the genus *Oenopota*, appear to be largely specialist vermivores (SHIMEK, 1983c). *Oenopota* species are abundant and common in Alaskan waters (BAXTER, 1981), and neptuneids may have faced substantial competitive pressure, which forced them away from specialization on polychaetes. Moreover, the large size of the neptuneids may require more energy input per unit time than a steady diet of small polychaetes alone can provide.

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Spatial Distribution of Three Species of Bivalves on an Intertidal Flat: the Interaction of Life-history Strategy with Predation and Disturbance

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Abstract. Spatial distributions of three species of bivalves, *Gemma gemma*, *Mulinia lateralis*, and *Mya arenaria*, were examined on a Delaware Bay intertidal flat inhabited by large numbers of horseshoe crabs, *Limulus polyphemus*. Populations within and outside of predator exclosures were compared. *Gemma gemma*, which has no actively swimming larval stage, was strongly aggregated after settlement. Larger individuals in protected plots remained aggregated, but in unprotected plots, there was some tendency toward randomization. *Mulinia lateralis*, which has planktonic larvae and actively burrowing juveniles, was most aggregated just after settlement. Protected individuals of *M. lateralis* were much more numerous, and were less aggregated, than unprotected *M. lateralis*. *Mya arenaria* also has a planktonic larval stage, but juveniles are somewhat less motile. Protected individuals were initially aggregated and remained so; predators eliminated nearly all unprotected *M. arenaria*.

INTRODUCTION

KNOWLEDGE OF THE spatial distribution of organisms is important to expedient sampling, and spatial patterns may also provide information on inter- or intra-specific relationships. Clumping or aggregation must be considered in designing a sampling strategy (GAGE & GEEKIE, 1973; MOORE & McLAUGHLIN, 1978; BOTTON, 1979; DOWNING, 1979). Spatial patterns may reflect physical variability in substratum, or be indicative of biological interactions. For example, spatial pattern in spionid polychaetes and its relationship to aggressive behavior was reported by LEVIN (1981).

Life-history strategies may influence spatial distributions of bivalves (BRADLEY & COOKE, 1959; MATTHIESSEN, 1960; JACKSON, 1968; GREEN & HOBSON, 1970; THOMPSON, 1982). Juveniles of species that brood larvae, such as *Gemma gemma*, may be aggregated (JACKSON, 1968; THOMPSON, 1982), as with a "seed shadow" about a parent tree. The spatial pattern of species with planktonic larvae is difficult to predict; hydrographic factors such as water temperature and salinity may influence the dispersion of larvae prior to metamorphosis, and conditions of the settlement surface, including the presence of predators, are also significant (THORSON, 1966; WOODIN, 1976). After settlement, waves and currents may redistribute bivalves (MATTHIESSEN, 1960; JACKSON, 1968; THOMPSON, 1982).

Predation may also influence the spatial distribution of bivalves. In theory in a heterogeneous environment, predators should concentrate their feeding in the richest patches, and remain until their net rate of energy intake in these patches falls to the average value for the habitat (HUGHES, 1980; SIH, 1982). Such "optimal patch use" predators should therefore equalize prey density among patches.

A caging study that excludes predators is a straightforward approach to studying the effect of predation on spatial distribution of bivalves within comparably sized caged and uncaged plots. SCHNEIDER (1978) found that shorebirds equalized the spatial dispersion of the prey on a Massachusetts mudflat. The present paper describes a cage study conducted on intertidal sand flats in Delaware Bay, New Jersey, in the spring-summer of 1978 and 1979. Population censuses of the horseshoe crab, *Limulus polyphemus* (Linnaeus) (BOTTON, 1984), and bird-exclosure treatments (BOTTON, 1983) strongly suggested that the principal predator and sediment disturber was *L. polyphemus*, which utilizes these beaches for several months for reproduction. Effects of caging on the abundance and size-frequency distributions of bivalves are considered in another paper (BOTTON, 1984). Here, I consider the influences of life histories, predation, and disturbance on the spatial patterns of the three most abundant species of infaunal bivalves, two with planktonic larvae—*Mya arenaria* Linnaeus, 1758 (Myacidae) and *Mulinia lateralis*

Table 1

Mean (\bar{x}) and Coefficient of Dispersion (CD) for the three most abundant bivalve species in the 1978 predator enclosure experiments, using 2 enclosures. * indicates aggregated distribution, based on the statistical procedure of CLARKE & MILNE (1955); otherwise, the distribution is random. Each mean and CD is based on 3 replicate 0.0048-m² cores.

Species	Date	Enclosure 1		Enclosure 2		Unprotected 1		Unprotected 2	
		\bar{x}	CD	\bar{x}	CD	\bar{x}	CD	\bar{x}	CD
<i>Mya</i>	6/8	12.3	0.9	8.0	5.3*	10.0	5.3*	1.7	3.3
	6/23	31.3	7.6*	19.3	3.5*	9.3	5.2*	5.7	1.1
	7/7	110.3	30.3*	44.0	4.1*	3.3	1.9	4.0	0.5
	7/20	42.0	3.9*	24.3	7.2*	0.0	—	1.3	0.2
	8/4	36.7	8.9*	25.7	1.7	0.7	0.3	0.3	0.7
<i>Mulinia</i>	6/8	48.7	2.3	86.0	19.2*	35.3	9.2*	33.0	12.2*
	6/23	142.7	35.2*	168.3	72.5*	60.0	21.6*	82.3	5.6*
	7/7	90.7	0.6	96.0	12.1*	59.3	17.2*	68.0	4.1*
	7/20	73.3	3.1	83.3	0.1	17.3	0.9	50.0	4.3*
	8/4	60.3	2.8	96.7	0.8	39.3	16.1*	18.3	0.6
<i>Gemma</i>	6/8	169.3	20.5*	77.7	21.4*	100.3	27.8*	24.7	7.6*
	6/23	100.7	9.7*	74.3	30.5*	31.7	7.7*	18.0	6.7*
	7/7	110.0	5.6*	96.3	51.6*	22.0	2.8	44.0	7.7*
	7/20	92.3	2.1	75.7	1.0	11.7	14.4*	19.3	2.1
	8/4	56.3	5.1*	37.3	0.8	13.3	2.2	15.7	3.9*

Linear regressions of Coefficient of Dispersion (y) on Mean (x):

Species	Intercept	Slope	r ²
<i>Mya</i>	0.86	0.23	0.810
<i>Mulinia</i>			
All data	-9.49	3.06	0.467
Less 2 highest	7.30	0.001	0.0003
<i>Gemma</i>	3.35	0.14	0.209

(Say, 1822) (Mactridae)—and one with direct development—*Gemma gemma* (Totten, 1834) (Veneridae).

MATERIALS AND METHODS

Field work was performed at the New Jersey Oyster Research Laboratory on the Cape May shore of Delaware Bay. Predator enclosures were 1.2 × 1.2 × 0.3 m wooden frames covered top and sides with large mesh wire (5.1 cm hexagonal openings in 1978, or 5.0 × 10.0 cm rectangular openings in 1979) to exclude shorebirds, large crabs, and fishes. The medium sand sediment (mean grain size = 0.38 mm, with <1% silt-clay) was not significantly altered by the cage (BOTTON, 1982).

To sample a cage, a 6-by-6 grid was painted on the side of the frame, and the location of a core was determined by rolling two dice. In 1978, three cores were taken from each of the two enclosures and three more from each adjoining unprotected plot on 8 June, 23 June, 7 July, 20 July, and 4 August. In 1979, four cores were taken from each of the three enclosures and from each unprotected plot on 16 April, 24 May, 14 June, 6 July, 20 July, and 3 August. Each cage plus its unprotected plot is hereafter referred to as a "site"; a distance of about 30 m separated the sites. Cores were taken with a glass jar, 7.8-

cm inside diameter (=0.0048 m²), which sampled to a depth of 10 cm. This core size was chosen because (1) the requisite number of replicates could be obtained without disrupting adjacent sediments or re-sampling a previous coordinate within the cage, and (2) prior qualitative sampling had revealed the small sizes and high densities of the infauna (see DOWNING [1979] on the relationship between benthos density, size of sampling devices, and number of replicates). Cores were washed through a 500- μ m mesh sieve, and the material retained was fixed in 10% formalin and transferred to 70% ethanol with rose bengal stain. Bivalves were enumerated and measured to the nearest 0.1 mm with an ocular micrometer or vernier caliper.

The spatial distribution of bivalve populations within sites was computed by the Coefficient of Dispersion (CD), which is the variance/mean ratio. This measure is based on the principle that for randomly distributed individuals, the mean number of individuals per core should equal the variance (Pielou, 1969). A CD significantly above one indicates that the population is aggregated, and values significantly less than one indicate a uniform dispersion. Statistical significance was based on the test of CLARKE & MILNE (1955), namely, a CD exceeding the confidence interval $1 + 2\sqrt{(2n)/(n-1)}$, where n is the number of

replicate cores used to sample each caged or uncaged plot. Bivalves with a CD within this boundary are considered to be randomly distributed.

RESULTS

In 1978, caged sediments contained a significantly higher density of individuals than uncaged sediments. This response resulted from the enhanced survival of the bivalves *Mya arenaria*, *Mulinia lateralis*, and *Gemma gemma* (Table 1, and BOTTON, 1984).

Mya arenaria was generally aggregated in cages, but randomly dispersed in uncaged sediments. Only the 1978 year-class was present on 8 June, based on the size-frequency distribution which showed a mean shell length less than 2 mm, with no individuals >5 mm (BOTTON, 1984). The spatial pattern of newly set *M. arenaria* was similar regardless of treatment (Table 1). From 23 June onward, *M. arenaria* was aggregated in all caged sediments, except for enclosure 2 on 4 August. In contrast, the few *Mya* surviving in unprotected sediments during July and August were randomly distributed. Pooling both caged and uncaged samples, most of the variability in the Coefficient of Dispersion was related to the mean (linear regression, $r^2 = 0.81$; Table 1).

Mulinia lateralis was even more abundant than *Mya arenaria*, but did not show the same spatial pattern. Only the 1978 year-class of *Mulinia lateralis* was present; when first sampled (8 June), mean shell length was 1.5 mm, and there were no individuals above 3 mm in length (BOTTON, 1984). On 8 June, the day that cages were put in place, *M. lateralis* was highly aggregated in three of the four areas (Table 1). On 23 June, caged individuals of *M. lateralis* were aggregated; on 7 July, only cage 2 was aggregated, but on 20 July and 4 August, all caged *M. lateralis* were randomly distributed. The responses of the uncaged areas were not consistent. Overall, excluding 8 June, *M. lateralis* was aggregated in 6 of 8 uncaged samplings, but only 3 of 8 caged samplings. There was a weak positive relationship between CD and mean, as shown by linear regression. When all data were considered, r^2 was 0.47; however, when the two highest means (168.3 and 142.7 individuals/core) were eliminated, r^2 was only 0.0003 (Table 1).

The spatial distribution of *Gemma gemma* was analyzed in two ways: (1) the population as a whole, i.e., by combining all size classes (Table 1), and (2) separate analysis of new recruits (<1.4 mm) and older individuals (>2.8 mm) (Table 2). In the first case, individuals of *G. gemma* from both caged and uncaged sediments were most aggregated early in the summer, i.e., when clams were smaller and more numerous. Only 21% of the variability in CD was related to the population size (Table 1). The spatial distribution of new set was most aggregated early in the summer (Table 2). Larger *G. gemma* showed a mixture of clumped and random distributions, regardless of treatment.

The results from 1979 were limited to *Gemma gemma*, because both *Mya arenaria* and *Mulinia lateralis* had nearly complete recruitment failures (BOTTON, 1984). On 16 April, there were few small *G. gemma*, as the population consisted mainly of survivors from the 1978 year-class (Table 2, and BOTTON, 1984). Large numbers of the 1979 year-class were retained on a 500- μ m sieve from 14 June onward, and small individuals of *G. gemma* were generally aggregated in both protected and unprotected sediments. Large *G. gemma* individuals in unprotected sediments were randomly distributed in 15 of 18 instances (Table 2). In contrast, protected large *G. gemma* individuals were clumped in 12 of 17 cases.

The mean coefficient of dispersal for small *Gemma gemma* was 15.05 and for large *G. gemma*, 6.05. Protected clams were more aggregated (mean CD = 14.51) than unprotected clams (mean CD = 6.82) (Analysis of Variance, $F = 6.85$, 1,5 df, $P < 0.05$).

DISCUSSION

Aggregation, as measured by the coefficient of dispersion (variance/mean ratio), varies with mean density (DOWNING, 1979), but not all the variability in CD can be explained by this alone; biological factors must be considered. The three species studied have important life-history differences with respect to reproductive mode, mobility, and vulnerability to predation and sediment disturbance (Table 3). *Gemma gemma*, which has direct development, may be considered as an "equilibrium" species, somewhat resistant to predation (SCHNEIDER, 1978; WOODIN, 1981). *Mulinia lateralis* and *Mya arenaria*, which recruit by planktonic larvae, are "opportunists," quite vulnerable to predation (VIRNSTEIN, 1977; BOTTON, 1984).

The clumped distribution of small *Gemma gemma* found in 1979 and the first month of 1978 is consistent with JACKSON (1968). Older individuals of *G. gemma* were randomly distributed in the unprotected areas in the 1979 study, in agreement with JACKSON (1968) and GREEN & HOBSON (1970), though THOMPSON (1982) found that most *G. gemma* adults (defined as >0.9 mm length) on a San Francisco Bay mudflat were aggregated. The aggregation of larger *G. gemma* within enclosures may be imposed by the clumping of newly released juveniles, and retained in the absence of predation or sediment disturbance. The Delaware Bay intertidal flats are unstable and are re-worked by horseshoe crab burrowing; thus, individuals of *G. gemma* are unlikely to remain in the vicinity where they set. Yet, the clumped distribution of unprotected <1.4 mm animals throughout 1979 suggests that either disturbance did not completely randomize the spatial pattern, or that continued release of juveniles overshadowed the impact of disturbance. The importance of predation to larger *G. gemma* is debatable, since several studies indicate that this species is not preferred prey to certain shorebirds (SCHNEIDER, 1978), crabs (WOODIN, 1981), or horseshoe crabs (BOTTON, 1982), whereas GREEN & HOBSON (1970)

Table 2

Spatial distribution of newly recruited (<1.4 mm) and older (>2.8 mm) *Gemma gemma* in the 1978 experiment (2 exclosures) and 1979 experiment (3 exclosures). CD = coefficient of dispersion; * indicates aggregated dispersion. Each mean and CD in 1978 was based on 3 replicate 0.0048-m² cores; 4 replicates were used in 1979. Sites 1 and 2 in 1978 were not the exact same location as 1979.

Date	<1.4 mm clams				>2.8 mm clams			
	Protected		Unprotected		Protected		Unprotected	
	Mean	CD	Mean	CD	Mean	CD	Mean	CD
8 June 1978								
Site 1	58.0	7.1*	44.3	15.0*	0.0	—	0.3	0.7
Site 2	30.0	7.0*	13.3	4.5*	0.0	—	0.0	—
23 June 1978								
Site 1	6.7	2.2	1.3	0.7	9.7	0.6	1.0	0.7
Site 2	4.7	3.6	1.0	0.0	0.7	1.3	0.3	0.7
7 July 1978								
Site 1	3.3	1.1	1.3	0.2	66.0	7.8*	7.0	1.2
Site 2	5.3	1.3	6.0	1.3	39.7	27.9*	9.3	4.6*
20 July 1978								
Site 1	3.7	0.1	1.3	2.7	77.3	3.6	5.3	7.0*
Site 2	4.7	0.9	4.7	0.6	58.7	0.6	8.3	2.0
4 August 1978								
Site 1	1.3	1.2	3.7	0.4	49.0	5.4*	3.7	0.1
Site 2	6.3	3.2	4.3	1.4	27.0	1.3	5.7	2.5
16 April 1979								
Site 1	0.3	1.0	0.3	1.0	4.5	1.3	5.5	2.5
Site 2	0.8	1.2	0.3	1.0	7.3	2.5	5.5	1.0
Site 3	0.3	1.0	0.5	0.7	2.3	0.7	6.0	1.8
24 May 1979								
Site 1	0.5	2.0	2.0	2.0	9.8	7.1*	2.5	0.7
Site 2	4.8	14.2*	7.8	17.2*	9.3	25.0*	4.5	1.6
Site 3	2.8	3.7*	1.3	1.3	3.8	3.5*	1.5	1.1
14 June 1979								
Site 1	2.5	0.7	6.5	4.6*	4.0	0.7	3.8	2.9*
Site 2	35.0	105.2*	12.8	14.7*	14.3	10.1*	3.5	2.4
Site 3	18.5	11.3	2.8	2.0	14.5	20.3*	2.5	1.7
6 July 1979								
Site 1	8.0	4.6*	13.5	1.5	6.0	1.9	5.5	1.3
Site 2	50.3	14.0*	27.3	10.7*	25.3	20.3*	7.0	1.6
Site 3	29.0	2.3	13.3	3.6*	14.5	8.5*	8.3	2.4
20 July 1979								
Site 1	43.0	15.9*	47.7	4.3*	27.3	14.5*	13.3	1.4
Site 2	147.0	54.0*	64.0	48.7*	45.0	13.8*	15.8	10.4*
Site 3	108.0	46.7*	41.5	55.1*	20.5	15.4*	11.8	15.0*
3 August 1979								
Site 1 ¹	57.8	13.0* ¹	12.5	0.7
Site 2	129.0	44.8*	105.3	11.3*	53.8	8.8*	26.8	1.8
Site 3	60.3	10.3*	60.5	1.5	32.3	6.3*	15.5	2.3

¹ Mean and CD not calculated because of the loss of one replicate.

and RECHER (1966) noted predation on this species by horseshoe crabs and shorebirds, respectively. Even when *G. gemma* individuals on the Cape May shore of Delaware Bay were as numerous as 206,000/m² (late spring, 1980), *L. polyphemus* contained an average of only 4.1 *G. gemma* per gut (BOTTON, 1982).

JACKSON (1968) found that *Mulinia lateralis* was ran-

domly distributed on the scale of 5 cm-by-5 cm replicates within a 0.25-m² area, and considered this a logical consequence of its reproduction by planktonic larvae. However, in the present study, the smallest *M. lateralis* individuals (those found in June, 1978) were the most aggregated. A possible explanation for the randomization in spacing among older caged clams could be movement

Table 3
Life-history characteristics of the three principal bivalve species.

Characteristic	<i>Gemma gemma</i>	<i>Mulinia lateralis</i>	<i>Mya arenaria</i>	References
Reproductive mode	Brooder; larvae released as fully shelled embryos at 375 μ m	Planktotrophic; larvae set at 210–230 μ m	Planktotrophic; larvae set at 200 μ m	SELLMER, 1966; LOOSANOFF <i>et al.</i> , 1966
Mobility	Strong, active burrower	Active; juveniles can "hop" to avoid crowding	Limited and decreases with increasing size	BRADLEY & COOKE, 1959; VIRNSTEIN, 1977; STANLEY, 1970
Vulnerability to sediment disruption	Low; reburrowed from 5–20 cm	High	High	BRADLEY & COOKE, 1959; VIRNSTEIN, 1977
Vulnerability to predation	Low	High	High	SCHNEIDER, 1978; VIRNSTEIN, 1977; BOTTON, 1982

of individuals from sediments packed with conspecifics and *Mya arenaria*. I have no direct evidence that this occurred, although VIRNSTEIN (1977) observed that *M. lateralis* would "hop" along the substrate to avoid very densely populated areas. *M. lateralis* is a thin-shelled and shallow-burrowing clam, making it vulnerable to predation; it is a favorite prey of horseshoe crabs (BOTTON, 1982) and blue crabs (VIRNSTEIN, 1977). Predation on uncaged *M. lateralis* had an important numerical impact, but it did not equalize the spatial distribution, as might have been expected if predators were optimal patch users (HUGHES, 1980).

Mya arenaria is not an active burrower, and juveniles up to ~10 mm often retain a byssal attachment to sand grains (personal observations). These factors may explain the difference in spatial pattern between protected *M. arenaria* and the more active *Mulinia lateralis*. Caged *M. arenaria* individuals were generally aggregated whereas *M. lateralis* assumed a random distribution after an initially clumped set. The spatial pattern of *M. arenaria* juveniles may be maintained in larger clams in the absence of perturbations. Few *M. arenaria* survived outside cages, and horseshoe crab predation probably accounted for most of the mortality (BOTTON, 1984). The randomization of unprotected *M. arenaria* may largely be a numerical artifact, since as the mean decreases, the more likely it is that a Poisson distribution (variance = mean) is approached (CLARKE & MILNE, 1955).

This study has shown the importance of predation, disturbance, and life histories to the spatial pattern of bivalves, but several questions remain unanswered. One factor that has yet to be elucidated is the possible impact of predation and disturbance on the spatial pattern of newly set spat, *i.e.*, during the interval between settlement and "recruitment" onto a 500- μ m sieve. Secondly, aggregation was defined on the basis of replicate core samples within

a small enclosure, but if "optimal patch use" predators are operating in this system, they may be doing so on patch scales larger than those studied here. There were some large differences in Coefficient of Dispersion and/or mean number of individuals between sites separated by approximately 30 m. The cause of this variation is not known: differences may have been the manifestation of slight variations in hydrographic factors, subtle differences in the substratum, or in the case of uncaged sediments, differential mortality resulting from variations in predation and/or disturbance pressure.

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Orientational and Anatomical Trends Related to Detorsion among Prosobranch Gastropods¹

by

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Abstract. Extant prosobranchs were placed into three groups based upon (1) the angle between the coiling axis of the shell and the antero-posterior axis of the foot during locomotion and retraction of the animal into its shell, (2) the angle between pallial water currents and the antero-posterior axis of the foot, (3) the relative proportions of the shell aperture, and (4) the manner in which the foot was folded during retraction. In Condition I (archaeogastropods and lower mesogastropods) the shell axis is at a 30 to 60° angle to the foot during locomotion and retraction, the pallial water currents are at a 60 to 85° angle to the foot, the shell aperture is nearly round, and the foot most often folds transversely during retraction. In Condition II (higher mesogastropods and neogastropods) the shell axis is at a 0 to 10° angle to the foot during locomotion but a 30 to 80° angle during retraction, the pallial water currents are at a 10 to 30° angle to the foot, the shell aperture is nearly round, but with a siphonal notch, and the foot most often folds transversely during retraction. In Condition III (higher mesogastropods and neogastropods) the shell axis is at a 0 to 10° angle to the foot during locomotion and retraction, the pallial water currents are at a 0 to 20° angle to the foot, the shell aperture is elongate, and the foot folds longitudinally during retraction.

INTRODUCTION

ALTHOUGH MUCH ATTENTION has been given to the geometry of gastropod shells, there has been relatively little work on the more subtle functional and orientational relationships of these secretions to the soft parts that produce them and to the environments within which they exist. NAEF (1913) was one of the first to investigate the ways in which shells of different shapes are carried by the animals secreting them, noting that shells of extant prosobranchs are asymmetrically deposited in drawn-out, helical patterns—the “typical” snail shapes. These he termed anisostrophic shells, which are in contrast to primitive isotrophic shells, such as those borne by the extinct bellerophonites. In that group the whorls lay in a single plane. Naef concluded that anisostrophic shells, in spite of their

asymmetry, are carried in balanced positions by two simultaneous adaptations. The first of these he termed regulatory detorsion, whereby the spire of the shell has become shifted toward the posterior end of the animal; the second is inclination, whereby the coiling axis has become tilted upwardly from its original horizontal position.

Naef outlined some theoretical evolutionary steps leading to regulatory detorsion, and more recent authors, most notable RISBEC (1955) and LINSLEY (1978a), observed that in those gastropods with shell spires directed posteriorly, regulatory detorsion approaches 90°. These are the more highly evolved snails in which the coiling axis lies virtually parallel with the longitudinal axis of the extended foot (MORTON & YONGE, 1964).

The development of anisostrophy, and the related appearance of regulatory detorsion and inclination, was accompanied by profound alterations in the disposition and anatomy of the pallial organs and reno-pericardial complex (NAEF, 1913; YONGE, 1947), primarily the reduction

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and final loss of the post-torsional right members of previously paired structures.

Beginning with Raup's development of a mathematical model for coiled shells (RAUP, 1961, 1966), there has been a renaissance in the study of the functional morphology of gastropod shells. VERMEIJ (1971) described the interrelationships between angle of inclination of the coiling axis and adaptive diversity of shell form. He found that the small angles of inclination characteristic of siphonate gastropods are related to a diversity of shell shape greater than that possible among more primitive forms with large angles of inclination. GRAUS (1974) reported a latitudinal gradient in the morphological diversity of shells and postulated that the greater diversity in tropical latitudes is a function of increased availability of calcium carbonate for shell deposition. LINSLEY (1977, 1978a, b) noted that gastropods with large angles of inclination are detorted less, better adapted to hard substrata, and have lower rates of locomotion than do gastropods with low angles of inclination. PALMER (1980) proposed that locomotion rates and shell form are but two of several co-evolving adaptations to different habitats. MCNAIR *et al.* (1981) found that gastropods with elongate apertures have elongate feet and are found primarily on soft substrata.

There has remained to be undertaken a systematic study of the magnitudes of regulatory detorsion and of its phylogenetic trends within the orders of the Prosobranchia. Moreover, relationships between regulatory detorsion, the proportions of the shell aperture, and mode of folding of the foot during retraction have not been considered by prior investigators. The present report describes some of the major evolutionary changes within the prosobranch framework in relation to these parameters.

Preliminary results of this study were presented to the American Society of Zoologists (GAINNEY, 1979).

MATERIALS AND METHODS

Living specimens of prosobranchs were collected at the following localities: Jupiter Inlet and Lantana Beach, Palm Beach Co.; Missouri Key and Long Key, Monroe Co.; Turkey Point and Alligator Point, Franklin Co. (all in Florida); Cape Elizabeth, Cumberland Co., Maine; and Bodega Bay, Sonoma Co., California. Additionally, living Indo-Pacific specimens of 30 species were observed by the junior author while on an expedition to Fiji in 1973 (Table 4). Precise angular measurements were not taken from the Fijian species. However, the position of the coiling axis of the shell with respect to the antero-posterior axis of the foot during locomotion and during retraction of the animal into the shell, as well as the manner in which the foot was folded during retraction, were noted. These initial observations provided the framework for our subsequent, more precise, measurements.

The following parameters were observed in living, adult specimens:

(1) The *locomotion angle* is the angle formed between

the antero-posterior axis of the foot and the coiling axis of the shell, projected onto the horizontal plane (Figure 1A). The locomotion angle was measured from above a snail as it crawled on a horizontal surface.

(2) The *retraction angle* is that formed between the longitudinal axis of the foot and the coiling axis of the shell after retraction of the animal into its shell (Figure 1B). Where the locomotion angle and retraction angle differ in a species, the retraction angle represents the degree of twisting of the shell relative to the median plane of the body after withdrawal. As a matter of practicality, the retraction angle was often measured as the head and foot emerged from the shell cavity. Either mode of observation yielded the same angular measurement.

(3) The *water-current angle* is the angle between the inhalant pallial water current and the longitudinal axis of the foot (Figure 1A). In species with siphonal notches in the shell, the angle was calculated from a line connecting inhalant and exhalant regions of the aperture; for forms with apertures that lack notches, the water-current angle was observed and measured with the aid of fine particles of graphite or carmine placed in the water surrounding the living specimens.

(4) The *proportions of the shell aperture* (b/a) were measured as follows: the "length" of the aperture (b) is the greatest linear dimension in an abapical-adapical direction, excluding the siphonal notch (Figure 1C); the "width" (a) is the greatest linear dimension perpendicular to the "length" of the aperture. As a result of procedural differences, the aperture ratios reported here are slightly larger than those described by VERMEIJ (1971). He defined "b" as the greatest linear dimension of the aperture coplanar with the coiling axis, and "a" as the greatest linear dimension perpendicular to "b." Our measurements relate to the full functional extent of the area passed through by the soft parts as they expand from and contract into the shell cavity. The dimensions of apertures of small species were measured with the aid of camera lucida drawings of the apertures.

(5) The manner in which the foot is folded during retraction into the shell was also noted (Figure 1B). Longitudinal folding refers to creasing of the foot along its longitudinal axis. Transverse folding refers to creasing of the foot along a line at right angles to its longitudinal axis and perpendicular to the plane of the sole.

OBSERVATIONS

We discerned three distinct arrangements in the orientations of shell and body among the prosobranchs we observed:

First, there was a group in which the coiling axis of the shell forms a wide angle with respect to the median plane of the head and foot. This angle is typically about 60°, and does not alter upon retraction of the body into the shell cavity.

Second, there was a group in which the coiling axis is

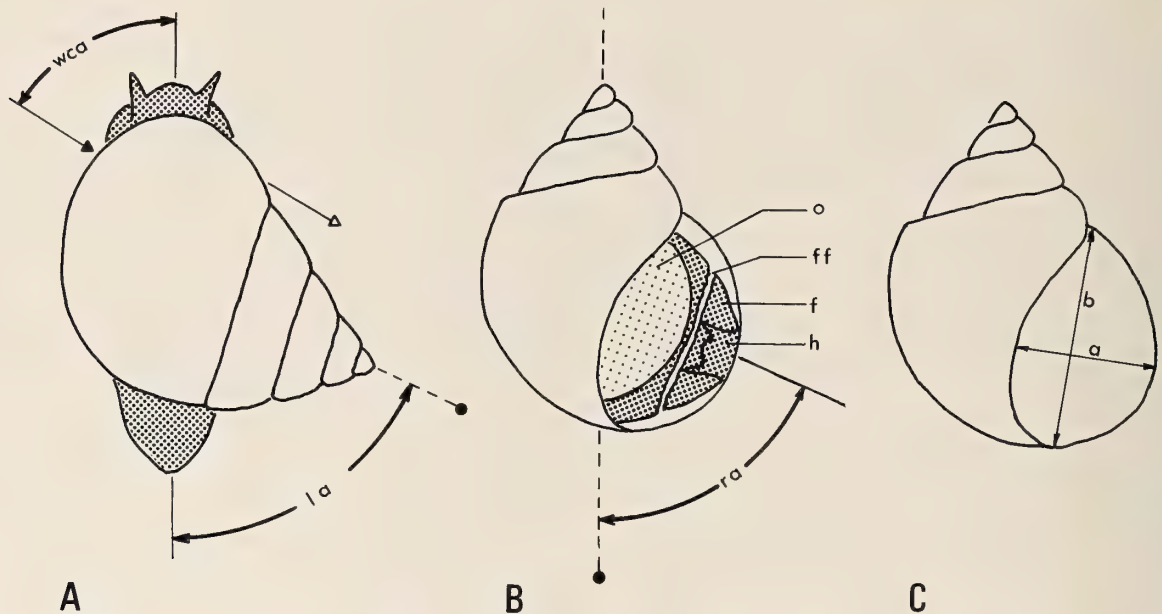


Figure 1

Oriental and anatomical parameters measured on living gastropods.

A: la, locomotion angle; wca, water current angle.

B: ra, retraction angle; ff, foot folding (transverse in this example); h, head; f, foot; o, operculum.

C: aperture ratio, b/a.

Solid arrow shows inhalant current; open arrow shows exhalant current. Solid lines mark antero-posterior axes of foot; dashed lines with terminal dots mark coiling axes.

parallel to, or forms an acute angle with, the median plane of the head and foot. This orientation is altered dramatically upon retraction.

Third, there was a group in which the coiling axis is virtually parallel to the median plane of the foot, an arrangement that does not alter upon retraction.

These situations form the basis for recognition of three conditions that involve not only shell-body orientations, but also the pallial water currents, proportions of the aperture, and modes of folding of the foot.

Condition I

All species exhibiting Condition I are archaeogastropods and non-siphonate mesogastropods (Tables 1, 4). Locomotion and retraction angles are the same and fell between 30 and 60°. That is, during locomotion the shell is carried obliquely at a fairly constant orientation with respect to the foot axis, and upon retraction the body and shell do not twist relative to one another.

There are two major arrangements with respect to ctenidial water currents. Most trochaceans possess incurrent and excurrent siphons formed by epipodial lobes, the former to the left, the latter to the right of the head. The angle between inhalant and exhalant streams is approxi-

mately 120°. In the remaining groups, the inhalant and exhalant water currents lie in a virtual straight line, which formed an angle ranging from 70 to 85° with respect to the longitudinal axis of the foot. Except for *Viviparus*, epipodial siphons are lacking in these forms.

Aperture ratios ranged from 0.9 to 1.8; thus, the aperture is broadly open. Among the archaeogastropods the aperture ratios averaged 1.2, whereas among the mesogastropods the average was 1.4.

The foot typically folds transversely as it is withdrawn into the shell aperture. There are exceptions (Figure 2a-d). In *Astraea longispina* and *Turbo castanea* the foot is withdrawn without folding. In *Calliostoma jujubinum*, *Tectus maximus*, *T. pyramis*, and *Trochus maculatus* the foot folds longitudinally. Among the latter three species, the folded ventral surface of the foot faces the outer shell lip at various angles, which affects the use or lack of use of the operculum in blocking the aperture.

Condition II

Many siphonate mesogastropods and some neogastropods are characterized by Condition II (Tables 2, 4). Among the mesogastropods, locomotion angles ranged from 0 to 40° (average 12°) and retraction angles from 30 to

Table 1
Species of gastropods typifying Condition I.

Animals	Locomotion angle	Retraction angle	Water-current angle	Aperture ratio	Foot folding
ARCHAEOGASTROPODA					
Trochidae					
<i>Tegula funebris</i> (A. Adams, 1855)	60°	60°	60°	1.1	transverse
<i>Calliostoma jujubinum</i> (Gmelin, 1791)	60°	60°	60°	1.3	longitudinal
Turbinidae					
<i>Turbo castanea</i> Gmelin, 1791	50°	50°	60°	1.2	none
<i>Astraea americana</i> (Gmelin, 1791)	50°	50°	63°	1.2	longitudinal
<i>Astraea phoebia</i> Roding, 1798	60°	60°	60°	0.9	none
<i>Astraea tuber</i> (Linné, 1767)	55°	55°	60°	1	none
Neritidae					
<i>Neritina reclinata</i> (Say, 1822)	60°	60°	75°	1.5	transverse
<i>Neritina virginea</i> (Linné, 1758)	60°	60°		1.4	transverse
<i>Nerita tessellata</i> Gmelin, 1791	60°	60°	80°	1.1	transverse
<i>Nerita versicolor</i> Gmelin, 1791	60°	60°	70°	1.2	transverse
MESOGASTROPODA					
Vivipariidae					
<i>Viviparus malleatus</i>	55°	55°	85°	1.4	transverse
Littorinidae					
<i>Littorina littorea</i> (Linné, 1758)	60°	60°	80°	1.3	transverse
<i>Littorina lineolata</i> Orbigny, 1840	60°	60°		1.3	transverse
<i>Littorina ziczac</i> (Gmelin, 1791)	60°	60°		1.6	transverse
<i>Littorina angulifera</i> (Lamarck, 1822)	30°	30°		1.4	
<i>Nodilittorina tuberculata</i> (Menke, 1828)	60°	60°		1.3	transverse
<i>Tectarius muricatus</i> (Linné, 1758)	60°	60°		1.3	transverse
Modulidae					
<i>Modulus carchedonius</i> (Lamarck, 1822)	60°	60°		1.3	transverse

60° (average 52°). Among the neogastropods, the locomotion angles ranged from 0 to 10° (average 2°) and the retraction angles from 30 to 80° (average 60°). In every species, the locomotion and retraction angles are unequal—there is a twist of the shell as the body retracts into its cavity. This twist is counterclockwise when the animal is viewed from above.

Those species that carry the shell with its axis subparallel to the locomotion angle (e.g., *Planaxis lineatus*) bear a short siphonal notch. The inhalant siphon, which extends from the notch, is carried in front of the head, or else is actively swept in an arc from side-to-side in front of the head during locomotion. Most of the species characterized by Condition II are capable of moving their shells in wide arcs during locomotion. This movement allows water to be drawn into the mantle cavity from a variety of directions and to “zero in” on sources of olfactory stimuli. In every case, water leaves the mantle cavity on the posterior right side of the organism.

The water-current angles listed in Table 2 were measured from specimens while their shells were being carried at the locomotion angles. The range of the water-current angles among the mesogastropods was 15 to 31° (average 24°), whereas among the neogastropods the range was 10

to 30° (average 15°). Although all species of Condition II are siphonate, the Potamididae lack a siphonal notch in the shell aperture.

The aperture ratios in these organisms ranged from 1.2 in *Urosalpinx perrugata* to 2.2 in *Terebra dislocata*, the average among the mesogastropods being 1.6, that among neogastropods 1.5.

During retraction into the shell cavity the foot typically folds once in the transverse plane (Figure 2f, l). Among the exceptions (Figure 2g, j-o) are *Cantharus cancellarius*, in which the foot is folded longitudinally, and species of *Terebra*. There is no folding in *Terebra dislocata* or in *T. duplicaria*, whereas in *Terebra maculata* and *T. dimidiata* there is an oblique folding of the foot.

Condition III

Some mesogastropods and some neogastropods represent Condition III (Tables 3, 4), characterized by a permanent disposition in which the coiling axis of the shell is subparallel to the longitudinal axis of the foot, whether during locomotion or after retraction.

On the average, the inhalant current enters the mantle cavity at 5° to the midline of the foot in the mesogastro-

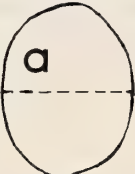
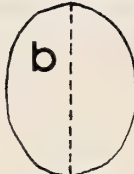
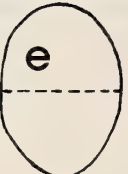
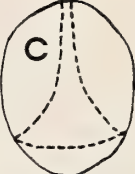

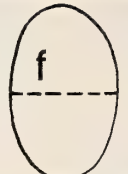
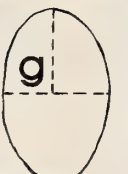

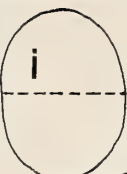






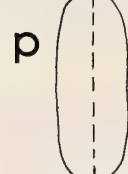
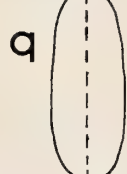
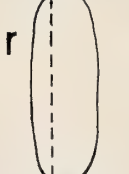

		ARCHAEOG.	MESOG.	NEOG.
CONDITION	I	 		
	II	 	  	      
	III			  

Figure 2

Some foot-folding patterns observed among prosobranchs; ventral views of sole. Anterior ends are upward in the diagrams. In instances of multiple creases, the anterior portions fold first upon retraction. Within each category, the presumed primitive state is shown first. a—(transverse) *Tegula*, *Nerita*; b—(longitudinal) *Tectus*, *Calliostoma*; c—(three flaps) *Nerita*; d—(no folding) some Turbinidae; e—Vivipariidae, Littorinidae, Naticidae, etc.; f—*Cerithidea*, *Cerithium*, *Cymatium*; g—Bursidae (unident. sp.); h—*Contumax nodulosus*; i—*Murex*, *Thais*, *Nassarius*, *Fasciolaria*; j—*Nassarius arcularius* (with lateral crumpling); k—*Cantharus*; l—*Latirus* (two lappets); m—*Terebra* (unident. sp.); n—*Terebra maculata*, *T. dimidiata*; o—*Duplicaria duplicaria*, *Terebra dislocata*; p—Cypraeidae, Cassididae; q—Columbellidae, Olividae, etc.; r—*Conus litteratus*, Mitridae; s—Conidae.

Pods, 14° in the neogastropods, and forms a virtual straight line with respect to the exhalant current, which is located far posteriorly on the right side of the body.

The shell aperture is always much longer than wide, the ratio averaging 6.7 for mesogastropods and 4.6 for neogastropods. The foot never folds transversely (Figure 2p–s), but either creases longitudinally or, as in species of *Conus*, simply slips unfolded along the columella into the shell cavity with the sole facing the outer lip of the shell.

We have not incorporated into our research a study of the operculum. However, it should be noted that the size of this structure, where present, and its position upon the foot are closely related to folding of the foot and to proportions of the aperture. In species with transverse folding, the operculum is attached to the section posterior to the fold, which retreats last into the aperture. This arrangement ensures closure of the opening by the operculum. Among forms with narrow apertures and longitu-

Table 2
Species of gastropods typifying Condition II.

Animals	Locomotion angle	Retraction angle	Water- current angle	Aperture ratio	Foot folding
MESOGASTROPODA					
Potamididae					
<i>Batillaria minima</i> (Gmelin, 1791)	0°	60°	30°	1.5	transverse
<i>Cerithidea costata</i> (daCosta, 1778)	0°	30°	31°	1.2	transverse
Cerithiidae					
<i>Cerithium eburneum</i> Bruguière, 1792	0–40°	50°	30°	1.3	transverse
<i>Cerithium muscarum</i> Say, 1832	0°	60°	30°	1.3	transverse
Planaxidae					
<i>Planaxis lineatus</i> (daCosta, 1778)	30°	60°	15°	1.8	transverse
Cymatiidae					
<i>Cymatium parthenopeum</i> (von Salis, 1793)	0°	60°	15°	1.5	transverse
NEOGASTROPODA					
Muricidae					
<i>Murex florifer</i> A. Adams, 1855	0°	60°	10°	1.4	transverse
<i>Urosalpinx perrugata</i> (Conrad, 1846)	0°	60°	10°	1.2	transverse
<i>Thais rustica</i> (Lamarck, 1822)	0°	60°	20°	2	transverse
<i>Nucella emarginata</i> (Deshayes, 1839)	0°	60°	10°	1.5	transverse
<i>Nucella lapillus</i> (Linné, 1758)	5°	70°	10°	1.7	transverse
Buccinidae					
<i>Cantharus cancellarius</i> (Conrad, 1846)	0°	30°	10°	1.7	longitudinal
Melongenidae					
<i>Melongena corona</i> (Gmelin, 1791)	0°	80°	10°	1.4	transverse
<i>Busycon contrarium</i> (Conrad, 1840)	0°	70°	10°	1.7	transverse
Nassariidae					
<i>Ilyanassa obsoletus</i> (Say, 1822)	10°	60°	20°	1.4	transverse
<i>Nassarius vibex</i> (Say, 1822)	10°	40°	20°	1.4	transverse
Fascioliariidae					
<i>Fasciolaria lilium hunteria</i> (G. Perry, 1811)	0°	60°	15°	2	transverse
Terebridae					
<i>Terebra dislocata</i> (Say, 1822)	0°	60°	20°	2.2	none

dinal foot-folds, the operculum is generally reduced or lacking. Independent trends toward reduction and loss of the operculum have taken place both in the mesogastropods (Cassididae, Cypraeidae) and in the neogastropods (Conidae, Mitridae) of Condition III.

CONCLUSIONS AND DISCUSSION

Observed prosobranchs fall into any one of three anatomical groups, here termed Conditions I, II, and III. Each condition is composed of features that may be analyzed separately, but are here interpreted as having evolved in closely interrelated fashions. Of the qualities concerned, orientation of the shell axis with respect to the extended foot, presence or absence of a twist of the shell over the foot during its retraction into the shell cavity, and the angle formed between pallial water currents and the axis of the foot were considered of primary importance in placing species in one of the three conditions. The relative proportions of the aperture and the manner in which the foot folds were considered of secondary importance, be-

cause there are overlaps and exceptions among these qualities within the three conditions. Typical arrangements are illustrated in Figure 3.

To set an evolutionary context for our observations, we agree with the view that modern gastropods found their origins in an extinct superfamily of archaeogastropods, the Bellerophontacea (Figure 3; see STASEK, 1972:26). These primitive forms were isostrophic and have been deduced to have possessed two bipectinate ctenidia, and hence paired reno-pericardial organs (NAEF, 1913; YONGE, 1947). The locomotion and retraction angles were probably 90°; that is, detorsion would have been 0° (Figure 3). There would have been no twist of the shell over the body during retraction. Moreover, the aperture ratio would have been low, a conclusion reached from illustrations in KNIGHT *et al.* (1960). If the foot folded at all during retraction, it was probably transverse to the longitudinal axis. Thus, based upon the parameters that define existing prosobranchs of Conditions I, II, and III, the bellerophonts would form another group—Condition "0" (Figure 3).

Steps away from bellerophont shell morphology in-

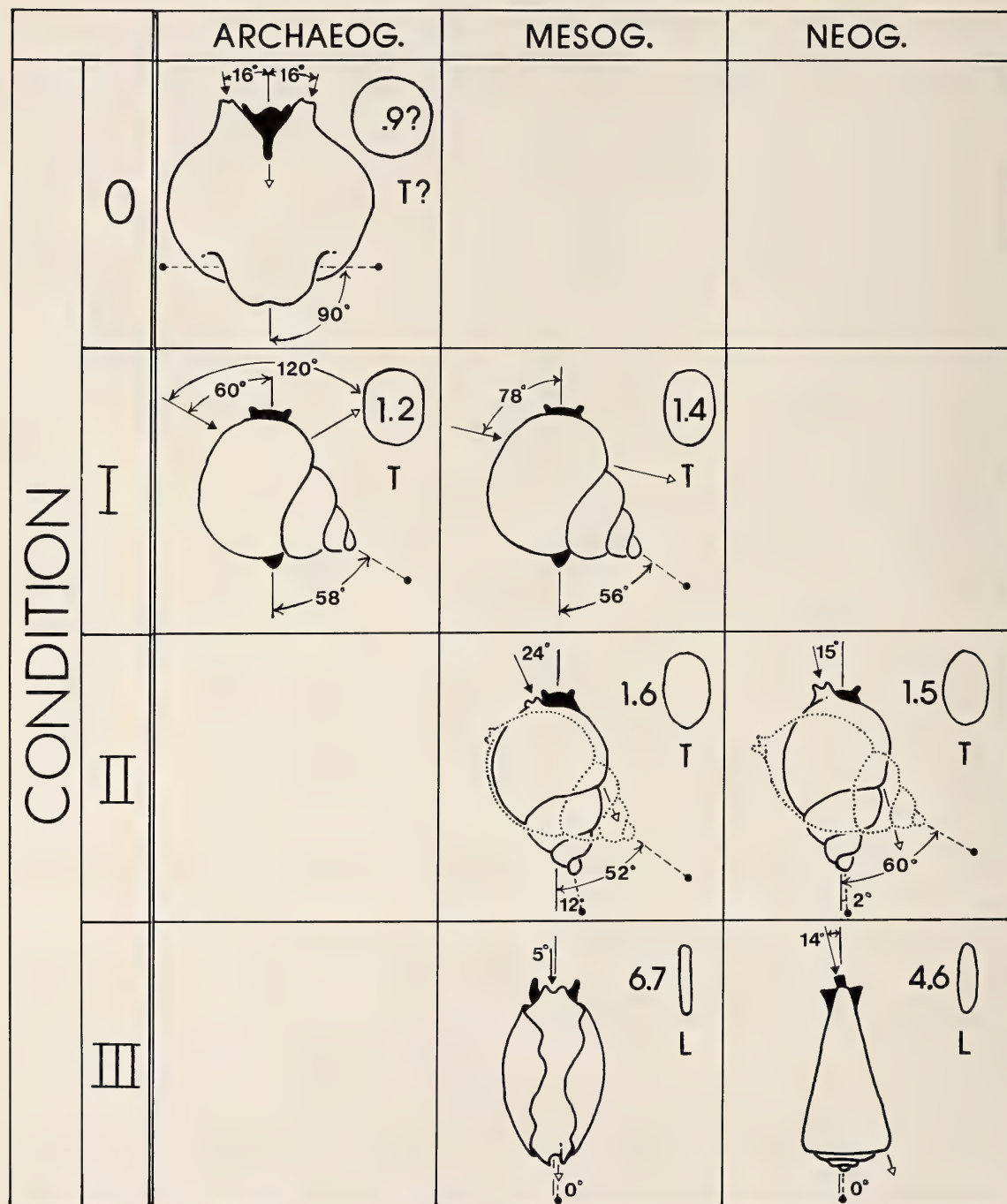


Figure 3

Summary of conditions relating locomotion, retraction, and water-current angles, aperture ratios, and foot folding among the prosobranch orders. Measurements are rounded-off averages from Tables 1, 2, and 3, except for the locomotion angle and retraction angle among the neogastropods of Condition III, for which measurements from *Mitrella lunata* have been excluded. Aperture ratios are indicated by ovals, not by outlines of actual apertures. Dotted outlines in Condition II represent the extent of twisting of the shell over the body upon retraction of the foot. The bellerophonts are represented in Condition "0" by *Knightites multicornutus* (modified from COX, 1960: 195). Solid arrows show inhalant currents; open arrows show exhalant currents. Solid lines mark antero-posterior axes; dashed lines with terminal dots mark coiling axes. L, longitudinal folding; T, transverse folding of the foot.

Table 3
Species of gastropods typifying Condition III.

Animals	Locomotion angle	Retraction angle	Water-current angle	Aperture ratio	Foot folding
MESOGASTROPODA					
Eratoidae					
<i>Trivia pediculus</i> (Linné, 1758)	0°	0°	0°	9	longitudinal
Ovulidae					
<i>Simnia uniplicata</i> (Sowerby, 1848)	0°	0°	0°	4	longitudinal
Cassididae					
<i>Cassis tuberosa</i> (Linné, 1758)	0–10°	0–10°	15°	7.2	longitudinal
NEOGASTROPODA					
Columbellidae					
<i>Columbella rusticoidea</i> Heilprin, 1887	0°	0°	11°	5	longitudinal
<i>Mitrella lunata</i> (Say, 1826)	10°	10°	16°	2	longitudinal
Olividae					
<i>Oliva sayana</i> Ravenel, 1834	0°	0°	6°	5.3	longitudinal
<i>Olivella pusilla</i> (Marrat, 1871)	0–5°	0°	20°	3.1	longitudinal
Marginellidae					
<i>Marginella apicina</i> Menke, 1828	0°	0°	10°	6.7	longitudinal
Conidae					
<i>Conus floridanus</i> Gabb, 1868	0°	0°	15°	7.8	longitudinal
Turridae					
<i>Cryoturris cerinella</i> (Dall, 1889)	0°	0°	20°	2	longitudinal

volved the formation of a spired shell, inclination of the coiling axis, and regulatory detorsion (NAEF, 1913; YONGE, 1947; LINSLEY, 1977). These qualities are borne by *Pleurotomaria*, regarded on anatomical grounds as among the most primitive living archaeogastropods. We have not observed *Pleurotomaria*, but we predict that it will have a locomotion angle of 60°, a shell and body that do not twist relative to one another during retraction, and a foot that folds transversely upon withdrawal into the shell cavity. These qualities would make *Pleurotomaria* a basic representative of Condition I.

The elements that comprise Condition I are found among recent non-patelliform archaeogastropods and non-siphonate mesogastropods. These animals are similar in their general appearance; detorsion ranges from 30 to 60°, and all of them have a rather high angle of inclination of the coiling axis (VERMEIJ, 1971). Moreover, most of them are grazers that are, with few exceptions, restricted to hard substrata. Based upon accepted views of gastropod phylogeny, we conclude that the qualities that define Condition I are primitive. To date, we have observed no neogastropods with the conformation of Condition I.

The mesogastropods and neogastropods characterized by Condition II bear shells the coiling axes of which are carried virtually parallel to the longitudinal axis of the extended foot. The inhalant and exhalant streams lie in a straight line, with the inhalant position much closer to the midline of the head than in forms typified by Condition I. These orientations alter upon retraction of the foot into the shell cavity in that the coiling axis swings counter-

clockwise when viewed from above. The twist of an average mesogastropod is about 40°; the shell moves even more, on the average, among the neogastropods. The species of Condition II are permanently detorted to about the same degree as those of Condition I, and temporarily detorted during locomotion by an additional 40 to 58° in mesogastropods and neogastropods, respectively. The orientation of the two axes in the retracted state is practically identical to the permanent arrangement of the more primitive forms characterized by Condition I.

As in Condition I, transverse folding of the foot during retraction is regarded as primitive, and the proportions of the length to width of the aperture of the shell are about the same as, or only slightly longer with respect to width, than those typical of Condition I. Species of *Terebra* are more variable in the matter of foot-folding than those of any other genus observed (Figure 3m, n, o).

Mechanisms relating to unequal locomotion and retraction angles vary within Condition II. In species with fusiform shells, the siphon is brought to an anterior position by muscular action, whereas species with high-spired shells that taper to slender points employ a purely passive mechanism (such as dragging on or in the substratum) to bring the siphon around in front (GAINNEY, 1976). Considering PONDER'S (1973) views on gastropod phylogeny, there has been convergent evolution of both fusiform and high-spired shells among mesogastropods and neogastropods.

The functional significance of high-spired shells is unclear. GRAUS (1974) noted that shells of this kind are

Table 4
Fijian species observed in relation to Conditions I, II, and III.

	Archaeogastropoda	Mesogastropoda	Neogastropoda
Condition I	Trochidae <i>Trochus maculatus</i> <i>Tectus maximus</i> <i>T. pyramis</i> Neritidae <i>Nerita</i> spp.	Littorinidae <i>Littorina</i> sp. Naticidae <i>Polinices pyriformis</i>	
Condition II		Cerithiidae <i>Contumax nodulosus</i> <i>Cerithium</i> sp. Bursidae "Bursa" sp.	Thaididae <i>Mancinella mancinella</i> <i>Morula granulata</i> Nassariidae <i>Nassarius arcularius</i> Fascioliidae <i>Latirus gibbulus</i> Terebridae <i>Terebra maculata</i> <i>T. dimidiata</i> <i>Duplicaria duplicaria</i>
Condition III		Ovulidae <i>Volva</i> sp. Cypraeidae <i>Cypraea tigris</i>	Olividae <i>Oliva mustellina</i> Mitridae <i>Mitra mitra</i> <i>Vexillum sanguisugum</i> <i>V. vulpecula</i> <i>V. gruneri</i> <i>Neocancilla papilio</i> <i>Pterygia dactylus</i> Conidae <i>Conus liratus</i> <i>C. arenata</i> <i>C. litteratus</i> <i>C. ebraeus</i>

usually confined to burrowing species, and he speculated that drag would be reduced as a result of elongation in the direction of locomotion. VERMEIJ (1977, 1978) observed that an increase in spire height reduces predation by calappid crabs, and that the appearance of antipredatory features of gastropod shells in the Mesozoic was paralleled by an increase in their predators. High-spined shells, for example those of the extinct Murchisoniacea and Loxonematacea, thought to be ancestral to the Cerithiacea (COX, 1960:143), are known from the Paleozoic, which would seem to preclude a solely antipredatory function of the shells of those groups.

The mesogastropods and neogastropods of Condition III exhibit a greater departure from the ancestral form than do those of Condition II. The temporary virtual alignment of shell and foot characteristic of Condition II is here permanent, with no twisting upon retraction. The angle at which the water current enters the mantle cavity with respect to the median plane is much more acute in the mesogastropods of Condition III, less so in the neogastropods. In keeping with the elongate apertures, which may be as much as nine times longer than wide, the foot

folds longitudinally as it is withdrawn, or slips unfolded into the shell cavity with the sole of the foot facing the outer shell lip. Again, there have been parallel evolutionary trends of these factors among mesogastropods and neogastropods. An additional factor in such parallelism has involved the probable independent appearance in the two higher prosobranch orders of inhalant siphons and of siphonal notches in their shells (PONDER, 1973).

FRETTER (1965) concisely summarized the anatomical arrangements found among the Prosobranchia, noting two major grades of organization—the Diotocardia, which we here term the Archaeogastropoda, and the Monotocardia, which is composed of the Mesogastropoda and Neogastropoda. Each of the latter two groups was considered by Fretter to represent an additional grade of organization. The conditions recognized in the present paper may also be considered grades of organization, but referring primarily to orientational relationships, rather than to anatomical conditions, as are those described by Fretter. Thus, Figure 3 represents a cross-indexing of anatomical grades in the vertical columns and orientational grades along the horizontal axis.

We have, then, the *anatomical* grade of the Archaeogastropoda, within which anatomical and orientational bilateral symmetry of the bellerophonts was lost through suppression of the post-torsional members of several previously paired organ systems and through the appearance of anisostrophy.

It was with the shell and body disposed in the *orientational* grade of Condition I that the Prosobranchia evolved the higher *anatomical* grades of organization: the monopectinate ctenidium, as well as the complete loss of right members of the pallio-renopericardial complex and the straightening out of the water currents. The primary taxobasis used by many to delineate the Mesogastropoda, the taenioglossate radula, made its appearance among forms characterized by Condition I.

Subsequent alterations in *orientational* relationships (that is, the temporary situation of Condition II and the permanent reorganization toward permanent external bilaterality of Condition III) took place independently within each of the higher two grades of *anatomical* organization. One, the Mesogastropoda, is extremely diverse, but with many herbivorous groups; the Neogastropoda consists mainly of carnivorous forms. Mode of feeding is, therefore, independent of orientational relationships, not only in Conditions II and III, but also in Condition I. It was with that primitive organization that the carnivorous Naticidae made their appearance.

There was, in the earlier stages of both the mesogastropods and neogastropods, some slight narrowing of the apertures (Condition II); but, independently in both those orders, the apertures became greatly elongated adaptically. There are several functional advantages that have been proposed for this elongation. For example, in the Conidae, Olividae, Volutidae, and Mitridae, various aspects of shell form, including an elongate aperture and foot, have been seen as adaptations to living on or in soft substrata (GRAUS, 1974; McNAIR *et al.*, 1981). VERMEIJ (1978, 1979) has presented extensive and convincing evidence that elongate shell apertures are particularly effective as a means of reducing predation, especially by crabs. It seems probable to us, as is the case in high-spined shells, that there are several adaptive advantages operating within the same species that would select for the traits characteristic of Condition III.

Finally, the primitive situation whereby the foot folds transversely during retraction into a broadly rounded aperture is replaced in both the mesogastropods and neogastropods by an elongate foot that either folds longitudinally or slips unfolded into a long, narrow aperture.

Orientation of the shell in relation to the body, positions of inhalant and exhalant water currents, retractor mechanisms of the foot, and proportions of the aperture of the shell have been shown to be interrelated attributes of gastropod functional anatomy. That the observed arrangements within any one order comprise a system of co-evolving elements is indicated by the parallelism that exists within the independent lineages of the Mesogastropoda

and Neogastropoda. At the same time that this clarifies some of the major evolutionary trends within the subclass Prosobranchia, we do not wish to imply "straight-line" phylogenies: that there has been convergent evolution and perhaps polyphyly finds much support. Yet, observed correlation of multiple traits reveals that we are dealing with matrices of co-evolving qualities, both anatomical and orientational.

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Reproductive Cycle of *Anomia simplex* (Pelecypoda: Anomiidae) from Cape Cod, Massachusetts

by

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Abstract. *Anomia simplex* from Woods Hole, Massachusetts, were studied for 24 months to determine the sequence of gametogenic development of gonadal tissue and the frequency and duration of the spawning cycle under natural conditions. These bivalves were observed to spawn annually in June–August after undergoing rapid gametogenesis. Sexes were distinguishable in all individuals examined, except those reported in an “inactive” condition. A low incidence of hermaphroditism suggests that *Anomia simplex* is a stable gonochoric species. Sex ratios of *A. simplex* did not differ significantly from 1:1 suggesting that protandry does not exist in this species. Photomicrographs of the gametogenic cycles of both male and female mussels are included.

INTRODUCTION

Anomia simplex (Say), the jingle shell, is a common bivalve of shallow waters from Nova Scotia to the West Indies. The valves of *A. simplex* are nearly translucent and, unlike most bivalves, they live permanently attached to solid objects by means of a stalklike byssus that passes through an opening in the lower valve. The cuplike upper valve commonly washes ashore after the animal dies and is one of the most abundant shells on many beaches. To date, the only information available on any aspect of the biology of *Anomia simplex* is COE's (1943a) histological study describing development of the primary gonads.

This study was designed to (1) define and categorize the sequence of gametogenic development based on microscopic examination of gonadal tissue and (2) determine the frequency and duration of the spawning cycle of *A. simplex* in a natural setting.

MATERIALS AND METHODS

Specimens of *Anomia simplex* were obtained from the Marine Biological Laboratory Supply Department, Woods Hole, Massachusetts. Individuals were obtained once a month during July, October, December 1981, February through September 1982, November 1982, and January through April 1983; twice a month during May 1983; three times in June 1981 and four times in August 1981. Sample sizes ranged from 10 to 20 individuals of variable shell size. A total of 412 bivalves was examined, of which

9 were immature. The remaining 403 mature individuals were used in the analysis of the reproductive cycle.

In the laboratory, the visceral mass of each individual was removed and fixed in 10% buffered formalin (HUMASON, 1967). The tissues were then prepared for histological examination (BROUSSEAU, 1978). A microscopic examination was made to assign each individual to the appropriate category of gonadal condition. Gonad color ranged from cream to dark orange, the darker shades appearing during the reproductively active months of the year. Photomicrographs of representative stages of the male and female reproductive cycle were taken with a Zeiss light microscope at 190× using a 35-mm camera. Panatomic X (ASA 32) film was used.

Mean oocyte diameter was determined for ten ripe females selected at random from each of the reported spawning periods. Twenty oocytes per individual were measured using an ocular micrometer. Only those oocytes that were spherical in shape and ready for release were selected for measurement.

The reproductive condition of the bivalves was measured by stereology, a procedure adapted by BAYNE *et al.* (1978) and NEWELL *et al.* (1982). This method is based on a procedure referred to as point-counting volumetry, which is accomplished by superimposing a regular point lattice on the tissue section and counting the points that lie on transections of the sex cells (WEIBEL *et al.*, 1966). The proportion of gonadal tissue that is composed of follicles containing developing or ripe gametes is reported as

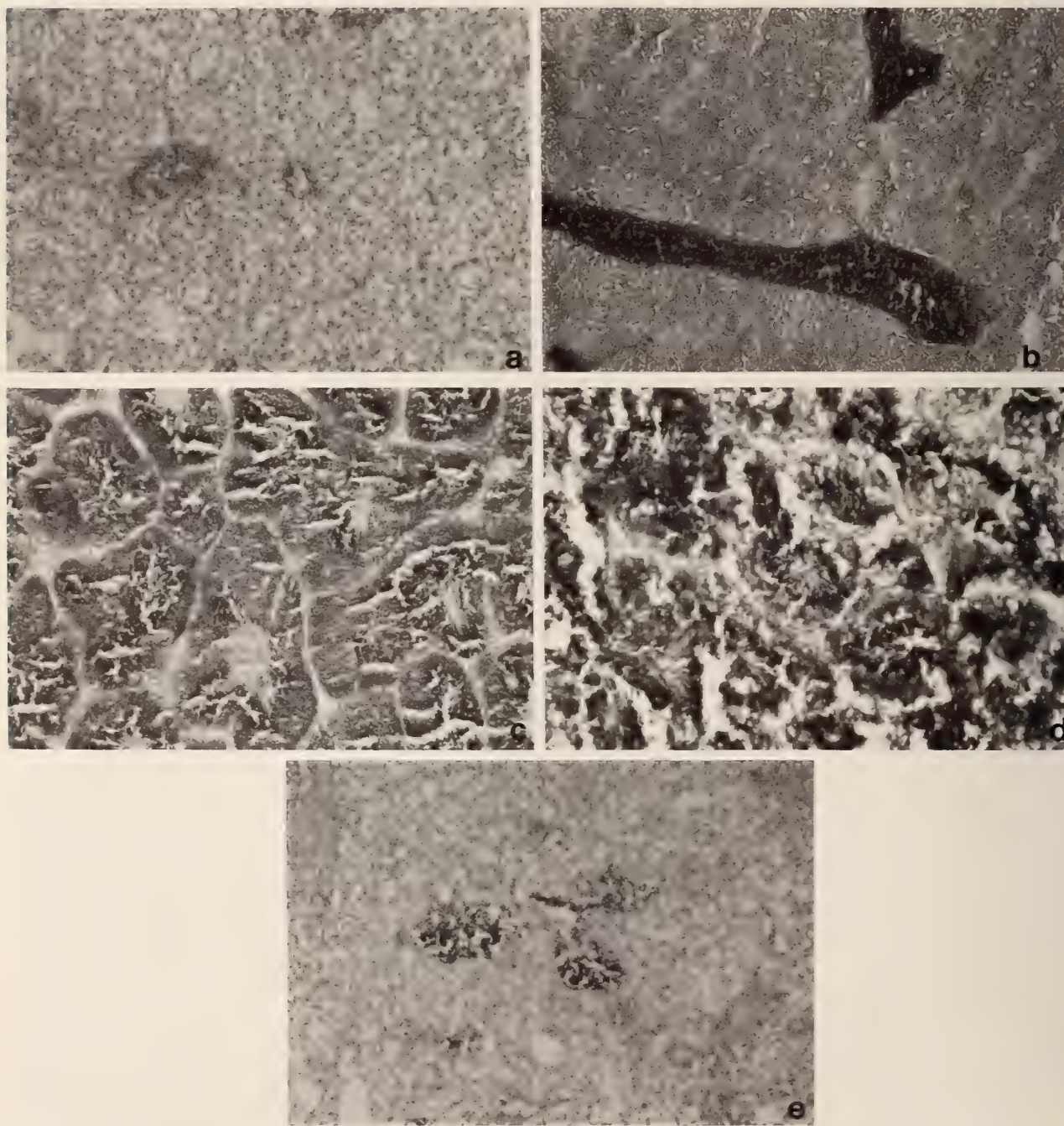
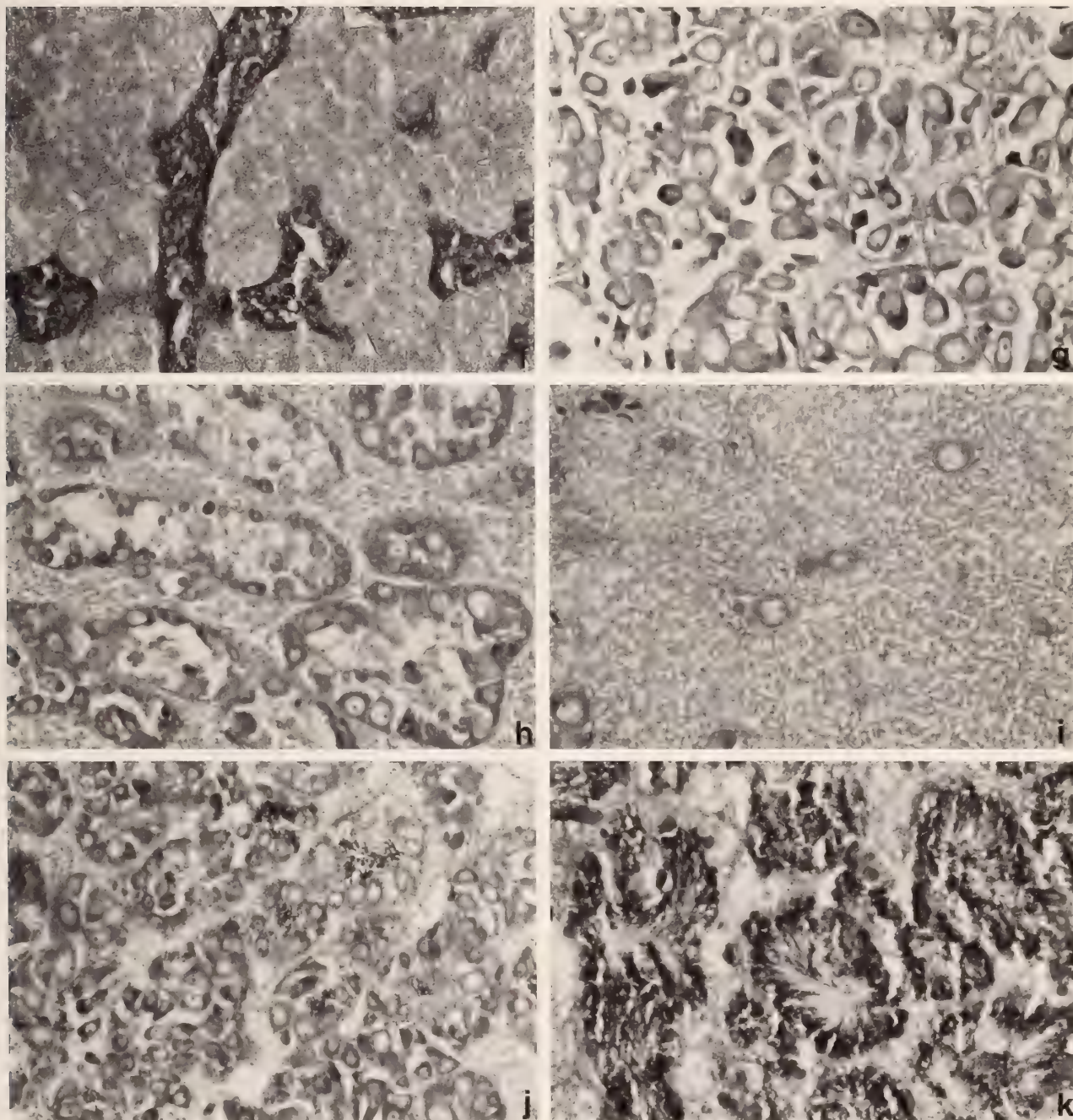


Figure 1

Photomicrographs of the gonadal stages of the male and female jingle shell, *Anomia simplex*, at 125 \times magnification. a. indifferent male or female, 18 August 1981; b. developing male, 27 May 1983; c. ripe male, 21 July 1981; d.

the "gamete volume fraction" (GVF). For any individual bivalve, the GVF can vary between zero, for a reproductively inactive individual, and one, for an individual showing maximal reproductive development. The monthly mean

GVF represents the mean of 10 estimates of the GVF from each individual sampled. These proportions were then arcsine transformed and the variance for each monthly GVF was calculated.



spawning male, 24 June 1981; e. recently spent male, 10 September 1982; f. developing female, 27 May 1983; g. ripe female, 21 July 1981; h. spawning female, 30 June 1981; i. recently spent female, 4 August 1981; j. hermaphrodite with female phase dominant, 21 July 1981; k. hermaphrodite with male phase dominant, 25 July 1982.

RESULTS

Categories of Gonad Condition

The following description of the male and female developmental stages represents an attempt to divide the

reproductive process (either spermatogenesis or oogenesis) into distinct phases. The criteria used are based solely on morphological observations. Categories comparable to those used for other species (ROPES & STICKNEY, 1965; BROUSSEAU, 1978, for *Mya arenaria*; PORTER, 1964; KECK

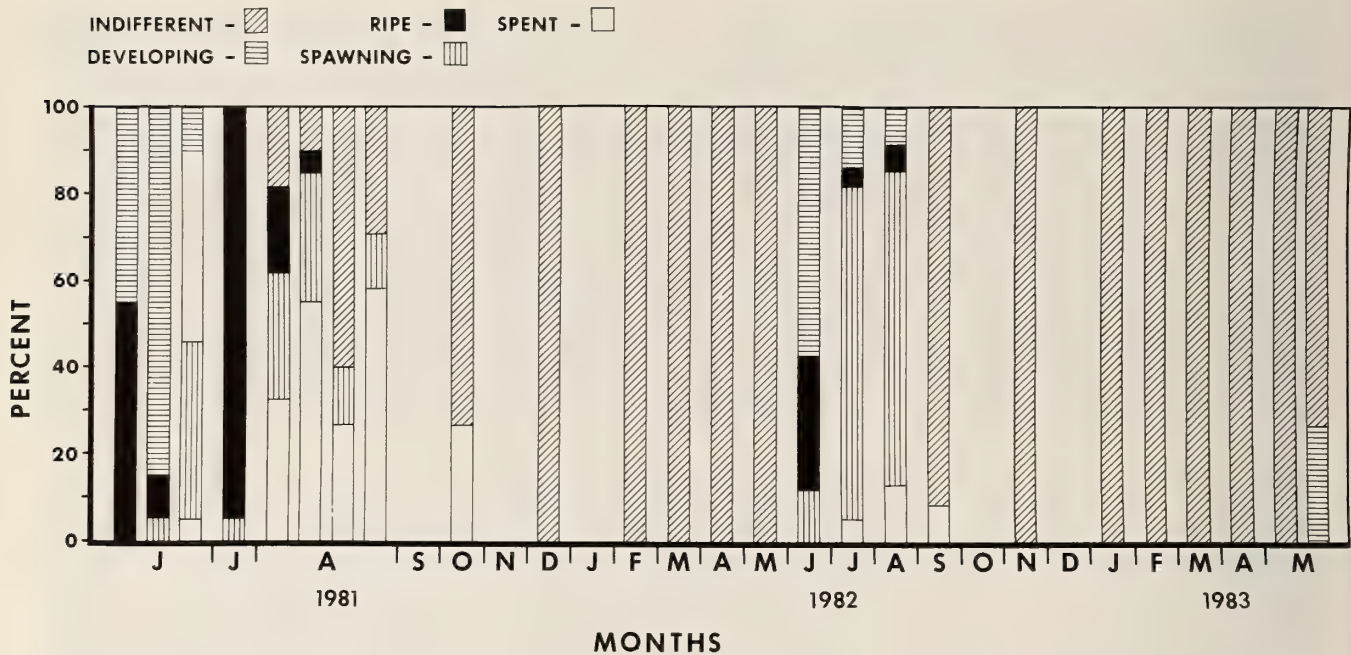


Figure 2

Proportions of male and female *Anomia simplex* with gonads in each developmental phase during 1981-1983.

et al., 1975, for *Mercenaria mercenaria*; BROUSSEAU, 1981, for *Petricola pholadiformis*; BROUSSEAU, 1982, for *Geukensia demissa*) were used in this study where appropriate.

Developmental Stages of the Male

Indifferent stage: The interfollicular space dominates, consisting almost entirely of vesicular connective tissue. The follicles are devoid of primary gonidia and the absence of gametogenic cells makes the sexes indistinguishable (Figure 1a).

Developing stage: The spermatogenic cells begin to proliferate around the follicle walls. A wide, centripetal band of spermatogonia, spermatocytes, and spermatids develops. The interfollicular connective tissue decreases with fewer large vacuolated fat cells being produced. The spermatids then differentiate into spermatozoa, which appear as a dense mass in the lumen of the follicle (Figure 1b).

Ripe stage: The mass of mature spermatozoa increases in volume and the individual cells arrange themselves into bands with tails pointing toward the center of the lumen (Figure 1c).

Partially spawned stage: There is a marked decrease in the number of spermatozoa filling the lumen, with most follicles empty or emptying (Figure 1d).

Spent stage: In the totally spawned male a few residual sperm are visible but the majority of follicles are empty. Spermatocytes are rare (Figure 1e).

Developmental Stages of the Female

Indifferent stage: The interfollicular space dominates, consisting almost entirely of vesicular connective tissue. The follicles are devoid of primary gonidia and the absence of gametogenic cells makes the sexes indistinguishable (Figure 1a).

Developing stage: Oocytes become more noticeable along the follicle walls, increasing in size and number. The developmental phase is a continuous process involving a proliferation and maturation of the oocytes, with an accompanying reduction in interfollicular connective tissue. Consequently, oocytes of various sizes and in various stages of development are present in the follicle simultaneously. The developing oocytes, which begin as hemispherical or cylindrical cells 10–20 μm in diameter and attached to the wall of the follicle, become enlarged spherical cells as maturity approaches (Figure 1f).

Ripe stage: Ripe females are characterized by the presence of large, round oocytes, 45–55 μm in diameter, some of which are attached to the follicular wall by slender stalks. Others appear as free oocytes in the lumen of the follicle. There is a very prominent eccentrically placed nucleolus visible within the nucleus (Figure 1g).

Partially spawned stage: There is a noticeable reduction in the number of ripe oocytes present in the lumen and some follicles are completely devoid of sex cells (Figure 1h).

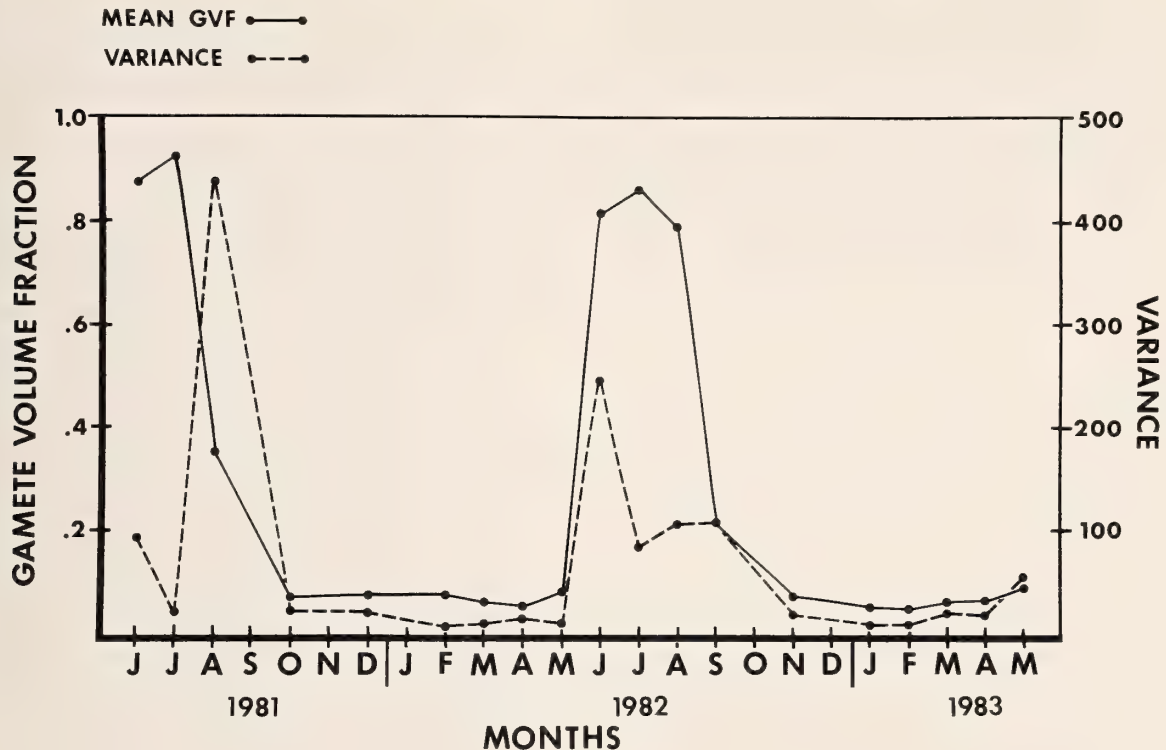


Figure 3

Mean Gamete Volume Fraction (solid line) and variance (dotted line) for male and female *Anomia simplex*.

Spent stage: Individuals that have recently undergone oogenesis can be recognized by the presence of a few unspawned oocytes in the lumen. These may be in various degrees of cytolysis. Resumption of oogenic activity may be evident in some individuals (Figure 1i).

Reproductive Cycle

Reproductively active individuals (Developing, Ripe, and Partially spawned) were encountered only during late May, June, July, and August of the two years studied (Figure 2). Gametogenesis in both sexes began in June of 1982 and in May of 1983. Fully ripe individuals were observed in the June samples of all years studied. Spawning began almost immediately and continued through the summer, with all of the gametes being released by August. By September, over 90% of the *A. simplex* had returned to the indifferent condition.

The "gamete volume fraction" (GVF) values for male and female individuals from this locale are shown in Figure 3. The pattern of GVF's and the maximum GVF attained were similar during both years studied. The post-spawning-reduced GVF's occurred in the early fall. Increasing GVF's due to the onset of gametogenesis were not evident until May or June of the years studied. Peak values of 0.87 were observed in July of both years. In

general, individuals of *A. simplex* were most closely synchronized (i.e., lowest variance) during fall, winter and spring months, when, according to evidence from Figure 2, most were in an inactive condition. With the onset of the reproductive period, the variance increased markedly, indicating that the bivalves did not all ripen and release gametes simultaneously. The breeding period of this species is so abbreviated, however, that this "apparent" asynchrony in spawning is in reality less dramatic in *Anomia simplex* than it is in other species such as *Mytilus edulis*, which spawns nearly all year (BROUSSEAU, in press).

Sex Ratios and Gonad Color

Out of the 185 individuals that could be sexed, the proportion of females in the population ($N = 87$) did not differ significantly from one-half. In nature, shell accretion in *Anomia simplex* is extremely variable, making it impossible to determine the size at which maturation is reached. It appears, however, that this species matures at a very young age since nearly all individuals sampled were mature. Hermaphroditism was observed in four individuals. From the evidence available, it appears that hermaphroditism is simultaneous, with both spermatogenic and oogenic cells produced in the same follicle. In half of the hermaphrodites inspected, the female phase dominated

(Figure 1j), whereas in the other half the male phase was more pronounced (Figure 1k). Hermaphrodites were collected in June, July, and August, and appeared to be undergoing normal gametogenic development.

Gonad color in *Anomia simplex* varies from cream to bright orange. Correlation between sex and gonad color, as has been reported for *Mytilus edulis* (CAMPBELL, 1969; BROUSSEAU, in press), could not be found in this species, however. Consequently, gonad color does not serve as a reliable indicator of sex in *A. simplex*.

DISCUSSION

Anomia simplex is a dioecious pelecypod, the sexes of which are distinguishable only after examination of the gonads. The low incidence of hermaphroditism exhibited by this species suggests that *A. simplex* possesses stable gonochorism, a condition characterized by the presence of some hermaphrodites in a normally gonochoristic species. The pattern of hermaphroditism exhibited by *A. simplex* is quite unlike that found in two related families, the Ostreidae (oysters) and the Pectinidae (scallops). In these latter two groups, hermaphroditism is well established. The scallops are among a group of strictly hermaphroditic pelecypods, whereas the oysters are often cited as the best example of hermaphroditic bivalves that undergo consecutive sexuality or protandry (COE, 1943b). *Anomia simplex*, on the other hand, is rarely ambisexual and, when such a condition is found, male and female sex cells are produced in the same follicle rather than in separate gonads or separate portions of a single gonad.

COE (1943a) describes the origin of the primary gonads in *Anomia simplex* from a pair of germinal primordia located in the posterior portion of the body. His description, however, does not include a discussion of subsequent gametogenic development in mature individuals. The evidence presented here suggests that the sex cells of *A. simplex* ripen quickly once gametogenesis begins. In 1982 ripe gametes were produced less than one month after gametogenesis began (Figure 2) and it seems likely that a similar pattern would have emerged in 1983 as well. The results of gonadal examinations indicate that *Anomia simplex* from Woods Hole, Massachusetts, spawn annually during the summer months. In general, North Atlantic species of marine bivalves tend to spawn during the warmer months of the year (SASTRY, 1979). Nonetheless, the reproductive period of *A. simplex* is considerably shorter than that of other notable North American shallow-water species such as *Mya arenaria* (ROPES & STICKNEY, 1965; BROUSSEAU, 1978), *Mercenaria mercenaria* (PORTER, 1964; KECK *et al.*, 1975), *Macoma balthica* (GILBERT, 1978), *Crassostrea virginica* (LOOSANOFF, 1937), *Spisula solidissima* (ROPES, 1968), *Mulinia lateralis* (CALABRESE, 1970), *Aequipecten irradians* (SASTRY, 1970), *Geukensia demissa* (BROUSSEAU, 1982), *Petricola pholadiformis* (BROUSSEAU, 1981), and *Mytilus edulis* (BROUSSEAU, in press). The rea-

son for this is not clear. Only after more information becomes available will it be possible to determine whether the spawning pattern reported here is characteristic of this species in all portions of its range.

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Influence of Varying Oxygen Tension on the Oxygen Consumption of the Freshwater Mussel *Lamellidens marginalis* (Lamarck) and Its Relation to Body Size

by

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Abstract. The oxygen consumption of the freshwater mussel *Lamellidens marginalis* is related to the oxygen tension of the medium. The total oxygen consumption increases, in general, with size irrespective of oxygen tension and with oxygen tension irrespective of body size. Variations in total and unit oxygen consumption as a function of oxygen tension are considerably less in smaller animals than in larger animals and both decrease drastically at very low oxygen tensions. From the P_c and oxygen-dependence index values it appears that smaller animals are more independent of environmental oxygen and tend to be regulators. Oxygen dependency increases with size, and larger animals show greater dependence of metabolism on oxygen tension and tend to be conformers.

INTRODUCTION

THE INFLUENCE OF declining oxygen tension on oxygen consumption has been studied in several marine and estuarine bivalves, but such studies on freshwater bivalves are relatively few. Most bivalves are supposed to be independent of oxygen tension down to a certain pressure below which oxygen uptake falls to very low levels (VAN DAM, 1938, 1954; GAARDER & ELLIASEN, 1954; ROTTHAUWE, 1958; NAGABHUSHANAM, 1962; BERG *et al.*, 1962; BAYNE, 1967, 1971, 1973; MOON & PRITCHARD, 1970; MANGUM & VAN WINKLE, 1973; MANGUM & BURNETT, 1975; TAYLOR & BRAND, 1975a; BAYNE *et al.*, 1976; WAITE & NEUFELD, 1977; BOOTH & MANGUM, 1978; DJANGMAH *et al.*, 1980; MACKAY & SHUMWAY, 1980). However, a few bivalves are oxygen conformers, with their oxygen consumption decreasing with declining oxygen tension (EDDY & CUNNINGHAM, 1934; HAMWI, 1969; BAYNE, 1971; LOMTE & NAGABHUSHANAM, 1971; RAO *et al.*, 1974; MANE, 1975; TAYLOR & BRAND, 1975a; McMAHON, 1979; FAMME & KOFOED, 1980; LOMTE & JADHAV, 1982).

The effect of body size on the relation between oxygen

uptake and oxygen tension has been studied in only a few marine bivalves, and the results are inconclusive (BAYNE, 1971; TAYLOR & BRAND, 1975b; FAMME, 1980; MACKAY & SHUMWAY, 1980).

Therefore, the relation between oxygen consumption and oxygen tension was studied in the freshwater bivalve *Lamellidens marginalis*, and the probable influence of body size on this relation was also investigated.

MATERIALS AND METHODS

The specimens collected from local streams were maintained in aquaria filled with water at the laboratory temperature of 26–28°C for 3–4 days to allow adaptation to laboratory conditions.

Oxygen consumption of the animals was studied using the apparatus designed by SAROJA (1959). The apparatus consists of a widemouthed bottle, serving as a respiratory chamber, fitted with a four-holed rubber cork. One inserted tube served as the inlet and connected to the reservoir, while another tube served as the outlet to collect samples. A third tube served as the control tube for maintaining the water level. A thermometer was fixed through the fourth hole for monitoring temperatures. The dissolved-oxygen content in the water samples collected from the apparatus before and after experimentation was determined by Winkler's iodometric method (WELSH &

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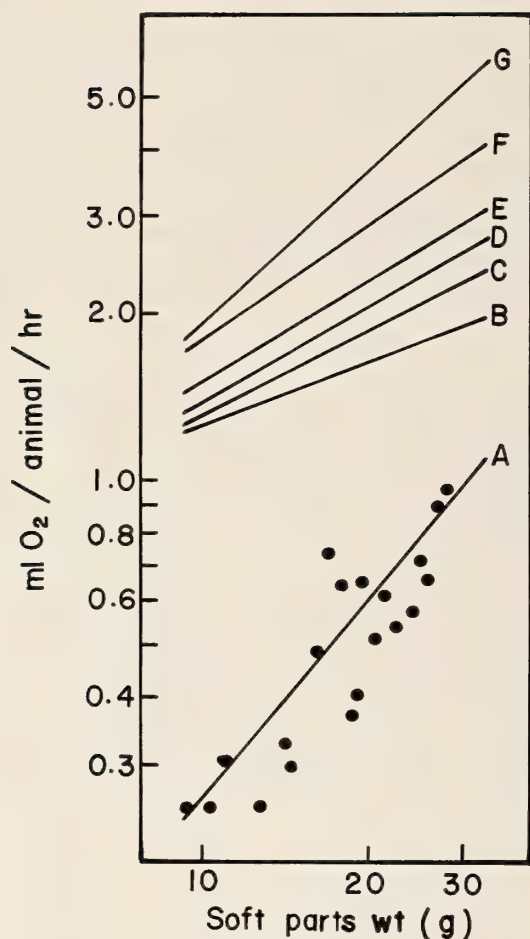


Figure 1

Total oxygen consumption ($\text{mL O}_2/\text{animal/h}$) in animals of different sizes measured at different oxygen concentrations of the medium. Temperature ranged from 26 to 28°C. Individual points are indicated for 'A' only. A, 1.13 mL/L ($\text{Po}_2 = 29.54 \text{ mm Hg}$); B, 2.83 mL/L ($\text{Po}_2 = 72.47 \text{ mm Hg}$); C, 3.87 mL/L ($\text{Po}_2 = 101.4 \text{ mm Hg}$); D, 4.91 mL/L ($\text{Po}_2 = 128.6 \text{ mm Hg}$); E, 5.57 mL/L ($\text{Po}_2 = 145.96 \text{ mm Hg}$); F, 7.56 mL/L ($\text{Po}_2 = 197.9 \text{ mm Hg}$); G, 10.20 mL/L ($\text{Po}_2 = 267.1 \text{ mm Hg}$).

SMITH, 1960). From the differences in the oxygen content, the total and unit oxygen consumptions were calculated.

Animals with soft-part weight ranging from 6–30 g were used to cover the natural size range. Animals were brushed thoroughly to remove algal growth over the shells before they were introduced into the respiratory chamber. The soft-part weight was determined at the end of experiments. Oxygen consumption was determined in oxygen-rich medium and then in media of successively decreasing oxygen concentrations. The oxygen content of the medium was changed by pumping either nitrogen or oxygen into it for decreasing and increasing the oxygen content of the medium, respectively. Experiments were carried out at the

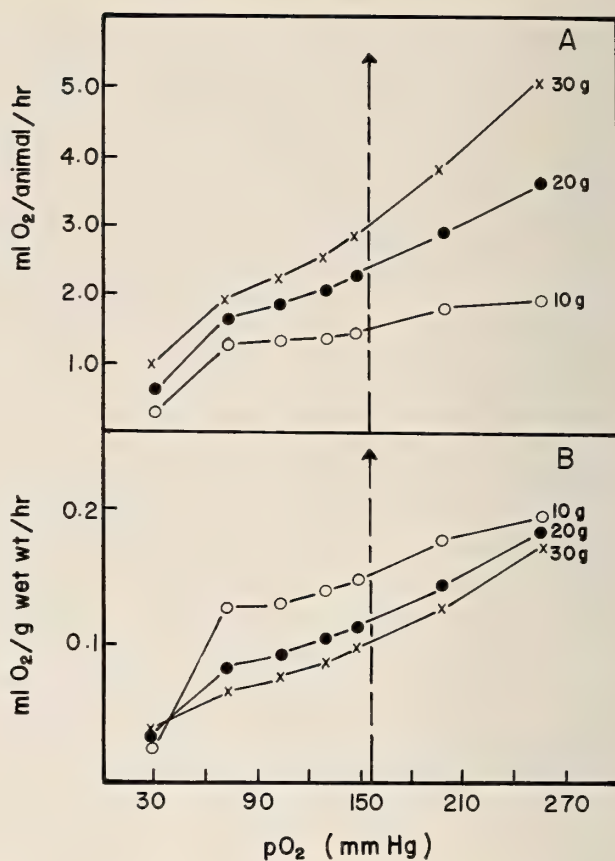


Figure 2

Total metabolism-oxygen tension (A) and unit metabolism-oxygen tension (B) curves plotted for animals of three sizes. Broken line indicates the oxygen tension at air saturation (26–28°C).

laboratory temperature of 26–28°C and in the afternoon hours so as to avoid diurnal variations.

Straight lines were fitted to the data plotted on a double logarithmic grid using the method of least squares. Other statistical analyses were carried out using standard procedures.

RESULTS

Oxygen consumption increased with oxygen tension irrespective of size and also with size irrespective of oxygen tension. However, the increase in oxygen consumption with size was not proportional and uniform at different oxygen tensions as indicated by the "b" values. The "b" values decreased gradually from 0.8968 to 0.3734 as oxygen content decreased from 10.2 mL/L to 2.83 mL/L . However, the "b" value increased greatly to 1.1119 when the oxygen content decreased further to the lowest value of 1.132 mL/L (Figure 1, Table 1).

The increase in total metabolism and decrease in unit metabolism as a function of body size were maintained at

Table 1

Regression analysis and correlation coefficient of variations in total metabolism in relation to size in *Lamellidens marginalis*, measured as a function of oxygen concentration (N = 20; level of significance = 95%).

	Oxygen content (mL/L)	Regression analysis		Standard error of b	Correlation coefficient (r)	Level of significance (P)	
		A (log a)	b			b	r
A	1.13	-1.6693	1.1199	0.2229	0.8165	<0.001	<0.001
B	2.83	-0.2731	0.3734	0.1189	0.6071	<0.01	<0.001
C	3.87	-0.4206	0.5246	0.0627	0.8085	<0.001	<0.001
D	4.91	-0.4281	0.5646	0.0843	0.7784	<0.001	<0.001
E	5.57	-0.422	0.5932	0.1246	0.8074	<0.001	<0.001
F	7.56	-0.4483	0.6935	0.118	0.8264	<0.001	<0.001
G	10.20	-0.613	0.8968	0.1561	0.833	<0.001	<0.001

all levels of oxygen tension (Figure 2). Furthermore, the variations in total and unit metabolism in relation to oxygen concentration were not proportional and linear, suggesting, thereby, some degree of independence of oxygen consumption on oxygen concentration. However, these variations were greater in larger animals and lesser in smaller animals. Furthermore, the oxygen consumption

was greatly depressed when the oxygen content decreased to the very low value of 1.32 mL/L, and this depression was highest in smaller animals. A critical tension or oxygen concentration (P_c) above which there was fairly good regulation of oxygen consumption was more prominent in smaller animals; it was not so clear as body size increased. It has been observed by earlier workers that P_c is not

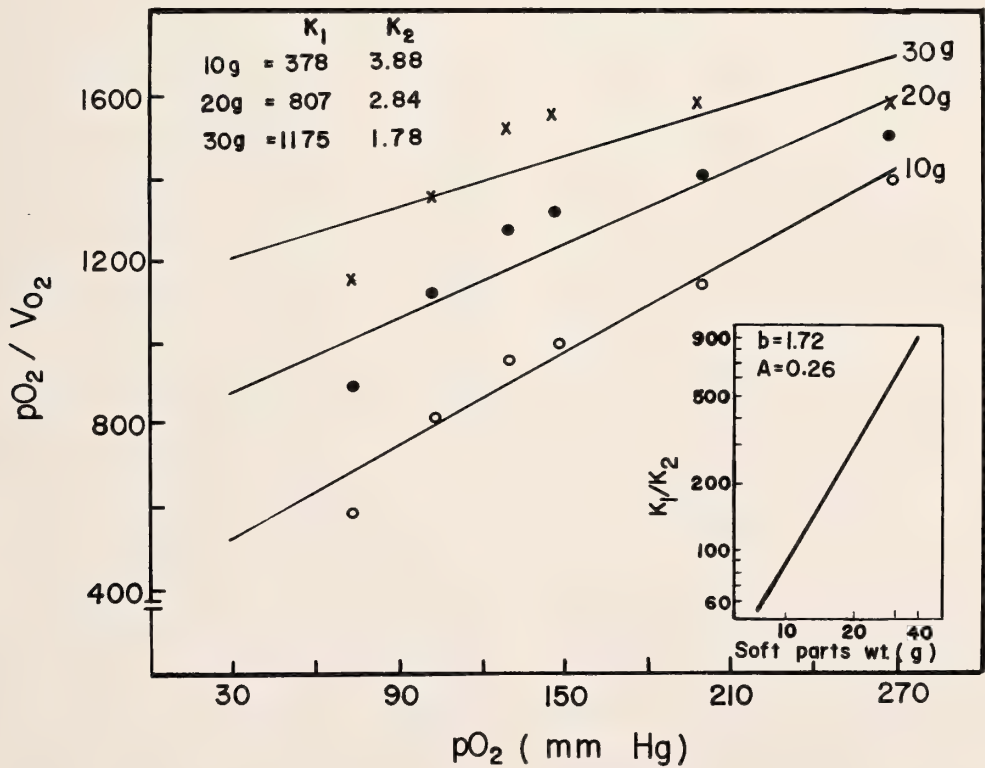


Figure 3

The relation between oxygen tension (PO_2) and the quotient of the oxygen tension and unit oxygen consumption (PO_2/V_{O_2}) in animals of three sizes (26–28°C). Inset shows the relation between oxygen dependence index and body size.

necessarily a sharp point in oxygen-regulating animals; the metabolism-oxygen curve is often hyperbolic (TANG, 1933). A more reliable estimate of oxygen dependence is obtained by plotting PO_2/VO_2 against PO_2 . Such a plot made for animals of three sizes showed linearity between the two variables. The linearity was not uniform, however, and decreased with increasing size (Figure 3).

The value of K_1/K_2 (where $K_1 = Y$ intercept and $K_2 =$ slope for PO_2/VO_2 versus PO_2 plots) provides an index of dependence of oxygen consumption on oxygen tension. Higher ratios indicate greater dependence. A plot of K_1/K_2 against body size indicated that the ratio increased with body size (Figure 3).

DISCUSSION

Aquatic animals respond to varying oxygen tension in the surrounding medium either by regulating or conforming their oxygen consumption. All kinds of responses of metabolism to oxygen tension are found in mollusks, ranging from total or partial dependence to complete independence (GHIRETTI, 1966).

Though oxygen uptake in marine bivalves such as *Katelysia opima* (MANE, 1975), *Congeria sallei* (RAO *et al.*, 1974), *Mercenaria mercenaria* (HAMWI, 1969), and *Mytilus edulis* (TAYLOR & BRAND, 1975a; FAMME & KOFOED, 1980) decreases with declining oxygen tension of the medium, imperfect regulation of oxygen uptake over a wide range of oxygen tension is evident in other marine forms. Among these imperfect regulators are *Mya arenaria* (VAN DAM, 1938), *Ostrea edulis* (GAARDER & ELIASSEN, 1954), *Pecten grandis* (VAN DAM, 1954), *Martesia striata* (NAGABHUSHANAM, 1962), *Mytilus perna* (BAYNE, 1967), *Mytilus californianus* (MOON & PRITCHARD, 1970; BAYNE *et al.*, 1976), *Laevicardium crassum* (BAYNE, 1971), *Gelonia ceylonica* (BAYNE, 1973), and *Arctica islandica* (TAYLOR & BRAND, 1975a). Both *Sphaerium simile* (WAITE & NEUFELD, 1977) and *Anadara senilis* (DJANGMAH *et al.*, 1980) are capable of regulating their oxygen consumption within certain limits of environmental oxygen. *Rangia cuneata* (MANGUM & VAN WINKLE, 1973; MANGUM & BURNETT, 1975) is a moderate regulator, whereas in both *Modiolus demissus* (BOOTH & MANGUM, 1978) and *Chlamys delicatula* (MACKAY & SHUMWAY, 1980) regulatory powers are poorly developed.

Information on the metabolic relations of freshwater bivalves to environmental oxygen is sparse. The available literature shows that *Anodonta imbecilis* (EDDY & CUNNINGHAM, 1934), *Parreysia corrugata* (LOMTE & NAGABHUSHANAM, 1971), *Corbicula fluminea* (MCMAHON, 1979), and *Corbicula regularis* (LOMTE & JADHAV, 1982) are conformers whereas good regulation of oxygen uptake is demonstrated by *Pisidium casertanum* (BERG *et al.*, 1962).

The present study shows that oxygen uptake by *Lamellidens marginalis* increases with the oxygen content of the medium irrespective of body size; but this increase is

not proportionate and the relationship is not linear, indicating that there is some degree of respiratory independence of oxygen tension, especially in smaller animals. However, at very low oxygen tensions, oxygen consumption decreases drastically, suggesting the breakdown of oxygen regulatory powers. A critical oxygen tension (P_c), above which there is fair regulation of oxygen consumption, is perceptible in smaller individuals, but not very clear in larger animals. The linear relationship obtained on replotting the data, as per TANG (1933), indicates the same. Thus, the freshwater mussel *Lamellidens marginalis* is neither a strict oxygen conformer like *Anodonta imbecilis* (EDDY & CUNNINGHAM, 1934), *Parreysia corrugata* (LOMTE & NAGABHUSHANAM, 1971), *Corbicula fluminea* (MCMAHON, 1979), and *Corbicula regularis* (LOMTE & JADHAV, 1982) nor a good regulator like *Pisidium casertanum* (BERG *et al.*, 1962). Rather, it shows some degree of metabolic independence of oxygen tension, leading to some regulation of oxygen consumption in relation to variations in ambient environmental oxygen.

Adequate information is not available regarding the influence of body size on the metabolism-oxygen relationship. Oxygen uptake in *Arctica islandica* is considered oxygen dependent, irrespective of body size (BAYNE, 1971); but a more recent study (TAYLOR & BRAND, 1975b) demonstrates a respiratory independence that increases with increasing body size. Similarly, the situation is not clear in *Mytilus edulis*: K_1/K_2 values decrease with size, indicating that larger individuals show less dependence on oxygen tension than smaller individuals (BAYNE, 1971), while K_m (oxygen dependence index) values suggest that oxygen dependence increases with body weight (FAMME, 1980). Lesser dependence on oxygen tension with size is also evident in *Laevicardium crassum*, where K_1/K_2 also decreases with size (BAYNE, 1971). A relation between the oxygen dependence index and body size is also shown in *Chlamys delicatula* (MACKAY & SHUMWAY, 1980).

The present study shows that the basic relation between metabolism and size is unaltered by oxygen tension. However, "b" values for total metabolism-size curves, and the metabolism-oxygen tension curves plotted for different size groups, indicate a greater influence of ambient oxygen tension on larger animals than on smaller animals. The increase in oxygen consumption with oxygen tension is less in smaller animals and more in larger animals. Interestingly, metabolism is depressed to a greater extent in smaller animals at low oxygen tensions, and this perhaps explains a steep increase in "b" value at low oxygen tension. Increased flattening of both total and unit metabolism-oxygen content curves with decreases in size also illustrates that oxygen uptake in smaller animals tends to be more independent of environmental oxygen and that a tendency toward conformity develops as body size increases, though a dependable correlation between P_c and body size is not evident. However, the linearity of lines plotted as per TANG (1933), and the increase in oxygen

dependence index (K_1/K_2) values with size, confirm that there is some degree of respiratory independence of oxygen tension and that this independence decreases with size. The present results agree with those on *Mytilus edulis* (FAMME, 1980) where respiratory independence also decreases with size, but they differ from those on *Mytilus edulis*, *Laevicardium crassum* (BAYNE, 1971), and *Arctica islandica* (TAYLOR & BRAND, 1975b) where respiratory independence increases with size. It is also clear that respiration is nearly surface-dependent at normal environmental oxygen tensions (4.91 to 7.56 mL/L), whereas it becomes nearly weight-dependent at extreme oxygen tensions (1.132 mL/L and 10.2 mL/L).

The fair degree of respiratory independence of oxygen tension observed in *Lamellidens marginalis* is of ecological significance. Low oxygen conditions are common in streams and ponds during summer months when water levels drop and the water becomes warmer and stagnant. In warm surface waters, both in freshwater and in the sea, there is much photosynthesis, and the oxygen concentration may exceed air saturation (PROSSER, 1973). Respiratory independence under conditions of such varying environmental oxygen would help the animals to maintain a fairly constant metabolic level. Quite interestingly, this ability seems to be better developed in smaller animals, implying that smaller animals can better withstand the rigors of environmental variations.

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Gaimardia bahamondei, spec. nov., from Central Chile (Mollusca: Bivalvia: Cyamiidae: Gaimardiinae)

by

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Abstract. The authors describe and illustrate *Gaimardia bahamondei* Osorio & Arnaud, spec. nov., from Isla Santa Maria (latitude 37°5'S; longitude 73°30'W), southeastern Pacific Ocean. Specimens were collected on the red alga *Gracilaria verrucosa* found at depths of 5 m. The new species is compared to those already known in the genus *Gaimardia* and its brooding habit is recorded. A new name is proposed for *G. exilis* H. & A. Adams, 1863, non Philippi, 1858: *G. adamsiorum* nom. nov.

INTRODUCTION

DURING FEBRUARY 1979, the commercial exploitation of seaweeds was hampered on the coasts of central Chile by a small prolific bivalve growing on the red alga *Gracilaria verrucosa*. The bivalve accounted for 20 and 52.3% of the total biomass harvested during February and September, respectively, around Isla Santa Maria.

The resulting lowering of the value of the algae drew our attention to this bivalve that we have identified as a new representative of the genus *Gaimardia* Gould, 1852, a genus characteristic of the southern oceans (ARNAUD, 1974). This bivalve is here described as *Gaimardia* (*Gaimardia*) *bahamondei* Osorio & Arnaud, spec. nov.

Bivalvia Linné, 1758

Cyamiacea Philippi, 1845

Cyamiidae Philippi, 1845

Gaimardia Gould, 1852

Gaimardia (*Gaimardia*) *bahamondei*

Osorio & Arnaud, spec. nov.

(Figures 1 to 5)

Description—shell morphology: Shell small (maximum length 7.7 mm), sub-ovate to sub-trapezoidal (Figures 1, 2), convex, thin, delicate, equivalve, and inequilateral. Beaks prosogyrate, prominent, anteriorly placed, and ad-

jacent. Periostracum salmon red, some individuals lighter red to white.

Anterior margin slanting, merging smoothly into the ventral margin through a blunt rostrum. Posterior margin uniformly rounded. Dorsal margin nearly straight. Ventral edge almost straight, sometimes with slight undulation at the point where byssus emerges. Without byssal gap, or with very narrow one.

Outer surface smooth, with tenuous and regular microscopic growth lines.

Hinge plate narrow. Two cardinal teeth on the right valve: the dorsal tooth triangular (Figure 3B) and the ventral tooth cylindrical and projecting (Figure 3A). Left valve with one cardinal tooth, elongated, wavy, anterior end rounded, fitting between teeth on right valve. Ligament dorsal, partially sunken, long, narrow, beginning behind the umbo (Figure 3).

Inner surface smooth, with faint muscle scars. Adductor scars slightly unequal: the anterior scar elongate, sub-oval, tapering to a pointed upper tip; the posterior scar less elongate and rounded. Anterior retractor muscle scar small, located close to upper edge of anterior adductor scar; posterior retractor scar coalesced with posterior adductor (Figure 4).

Description—anatomy: Mantle thin, transparent, smooth, and thickened at the edges which are joined by a membrane leaving three openings: anterior or pedal opening

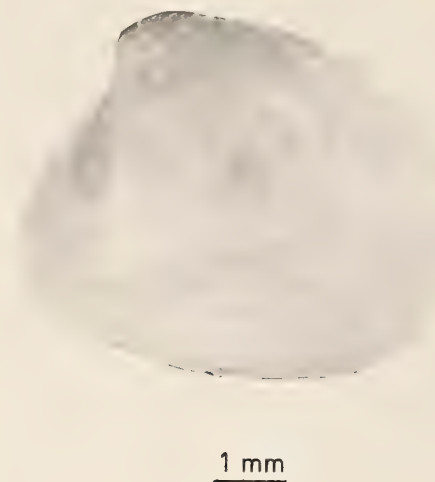


Figure 1

Gaimardia bahamondei Osorio & Arnaud, spec. nov.

medium sized; median or branchial opening almost twice as long as pedal opening; and posterior or anal opening about half as long as pedal opening (Figure 4). Sutures between these three openings are subequal in length.

Gills large, unequal, developed on both sides. Outer demibranch, elongate dorso-ventrally, and having a pointed posterior tip (Figure 4). Inner demibranch sub-quadrangular, nearly twice the size of the outer. Demibranchs joined posteriorly, anterior edges free. Both demibranchs are used for incubation of the eggs and juveniles.

Foot moderately developed, linguiform, directed anteriorly (Figure 4). The byssal gland is open at its posterior part, the byssus being formed by few very thin, translucent white fibers.

The anatomy of *Gaimardia* was studied or discussed, mostly in *G. trapesina* (under various names), by J. E. GRAY (1854), M. E. GRAY (1857), PELSENEER (1903), IGEL (1908a, b), ODHNER (1924), and PONDER (1971). The anatomy of the new species is in general agreement with that previously described in these other representatives of the genus.

Type locality: Chile, Isla Santa Maria (37°5'S; 73°30'W) in the Golfo de Arauco, near Concepcion, 4.5 to 5 m deep, on the red alga *Gracilaria verrucosa* (Hudson), March 1979.

Type material: **Holotype**—6.7 mm long × 5.0 mm high. Museo Nacional de Historia Natural, Santiago de Chile. No. ML 100244.

Paratypes—12 specimens 2.6–6.0 mm long, Museo Nacional de Historia Natural, Santiago de Chile, No. ML 100235. Other paratypes are deposited in Museum National d'Histoire Naturelle, Paris, France; U.S. National Museum, Washington, U.S.A.; Los Angeles County Museum, U.S.A.; and British Museum (Natural History), London, U.K.

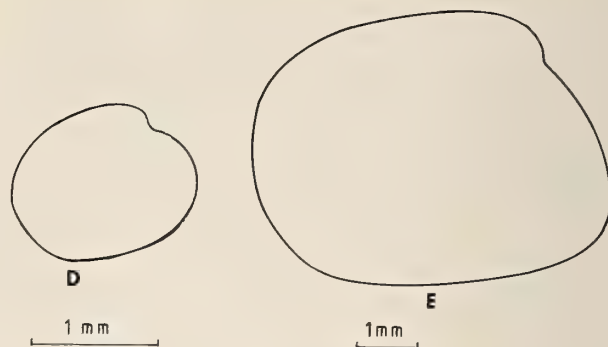


Figure 2

Variation of the outline of *Gaimardia bahamondei*, from sub-oval (D) to sub-trapezoidal (E), during its growth.

Etymology: This new species is kindly dedicated to Professor Nibaldo Bahamonde, investigator at the Museo Nacional de Historia Natural and Professor at the Universidad de Chile, in recognition of his work.

Biological notes: The size of specimens we have examined varies from 1.3 mm long × 1.1 mm high to 7.7 mm long × 6.0 mm high. The specimens tend to become trapezoidal in outline as their size increases (Figure 2). The size structure of the population (Figure 5) indicates the presence of juveniles (less than 4 mm in length) and adults between 4 and 7 mm long; adults account for about 75 per cent of the population.

Individuals are reproductive from 4 to 7 mm in length. In the inner demibranchs, we counted as many as 949 broods in a single female 7 mm long. The size of broods varies between 130 and 430 μm. A similar brooding habit is well known in the *Macrocystis*-associated *G. trapesina*.

Status of the subfamily Gaimardiinae: The genus *Gaimardia* was formerly considered as part of the family Gaimardiidae among the superfamily Gaimardiacea (see FLEMING, 1969). PONDER (1971) has shown that it is preferable to regard this family as a subfamily in the Cyamiidae of the superfamily Cyamiacea. This proposal has been recently questioned by MORTON (1979), but we accept it until more evidence is available.

Among the genus *Gaimardia*, three subgenera may be distinguished: the primitive subgenera *Neogaimardia* Odhner, 1924 (see MORTON, 1979) and *Progaimardia* Ponder, 1971, and the more evolved subgenus *Gaimardia* (s.s.).

Comparisons of *G. bahamondei* with other species: Our material from Isla Santa Maria was compared to the various representatives of the genus *Gaimardia* and related genera. This was done on the basis of examination of type material preserved in the Museum National d'Histoire Naturelle, Paris (types of Rochebrune and Mabilie) and in the British Museum (Natural History), London (types

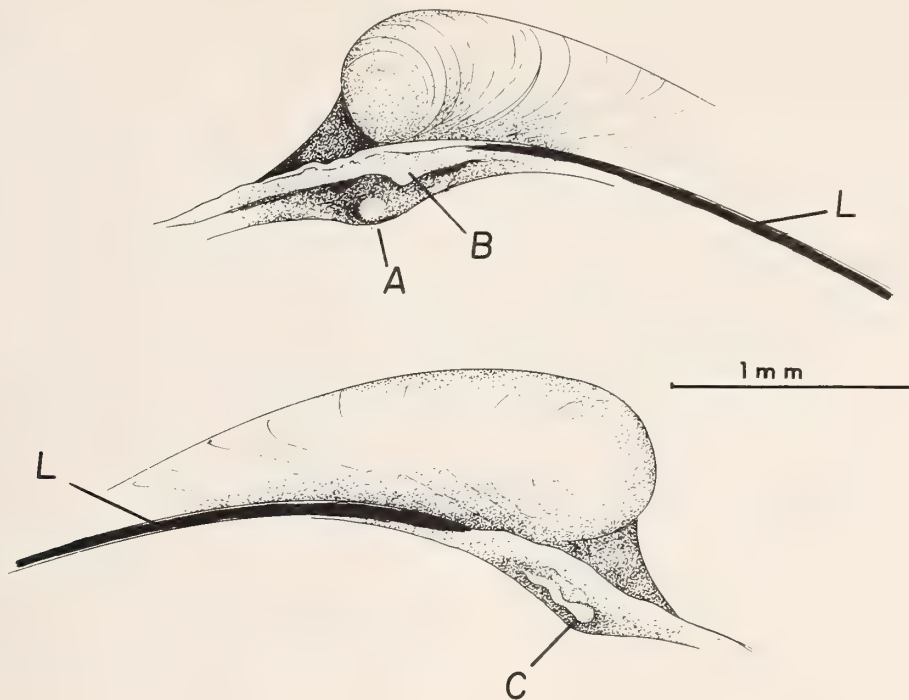


Figure 3

Gaimardia bahamondei Osorio & Arnaud, spec. nov., hinge region of both valves. Right valve: A, dorsal cardinal tooth; B, ventral cardinal tooth; L, ligament. Left valve: C, cardinal tooth; L, ligament.

of H. & A. Adams and Preston); we compared these types to recent samples from Kerguelen and Crozet Islands. It is obvious that the species from central Chile does not belong to the primitive subgenera *Neogaimardia* Odhner, 1924 (see MORTON, 1979) or *Progaimardia* Ponder, 1971, both having well developed hinges. *Gaimardia bahamondei* Osorio & Arnaud, spec. nov., is a member of the subgenus *Gaimardia* (s.s.) and more-or-less intermediary in all its characteristics between *Gaimardia* (*Gaimardia*) *exilis* (H. & A. Adams, 1863) and the much more-evolved *Gaimardia* (*G.*) *trapesina* (Lamarck, 1819).

Coincidentally we must rename this *Gaimardia exilis* (H. & A. Adams, 1863): another species, *Phaseolicama exilis* Philippi, 1858, has to be accepted into the genus *Gaimardia* (because *Phaseolicama* Rousseau, 1854, is a junior synonym of *Gaimardia* Gould, 1852: see, for example, FLEMING, 1969). So we propose to rename *Gaimardia exilis* H. & A. Adams non Philippi: *Gaimardia adamsiorum*, nom. nov.

The species from central Chile may be distinguished from *Gaimardia adamsiorum*, nom. nov. (redescribed and figured by SMITH, 1877, and PONDER, 1971, and available to us from the Falkland Islands as type material, and from the Kerguelen Islands) by several characters: *G. bahamondei* has a blunt rostrum, a thin shell, comparatively small cardinal teeth (however, they become more and more

indistinct with age in *G. adamsiorum*), and lacks lateral teeth.

Gaimardia trapesina is a variable species that has received many names (see, for example, DELL, 1964), including the following based on material from southern South America or South Georgia Island: *Phaseolicama magellanica* Rousseau, 1854; *Modiolarca nigromarginata*, *M. subquadrata* and *M. faba* Pfeffer, in Martens & Pfeffer, 1886; and *M. crassa*, *M. lecannelieri*, *M. lephayi*, *M. savatieri*, *M. fuegiensis*, *M. sauvineti* and *M. hahni* Rochebrune & Mabille, 1889. But the new species differs from *G. trapesina* by the following characters: a poorly-marked rostrum (always well-developed in *G. trapesina*), the cardinal teeth (very inconspicuous in *G. trapesina*), and the relative length of the three mantle openings. In *G. trapesina* the two ventral openings are subequal and separated by a suture longer than either; the anal opening is smaller (half the length of the other two openings). Other less diagnostic characters are the size of the foot (less developed in *G. bahamondei*), the color of the shell (salmon red as opposed to yellowish, brown or purplish brown in *G. trapesina*), and the habitat (*G. trapesina* being epibiotic on the large kelp *Macrocystis pyrifera*).

Gaimardia exilis Philippi was described without illustration, and we failed to trace the type material. At this stage, its true nature must be questioned, but according

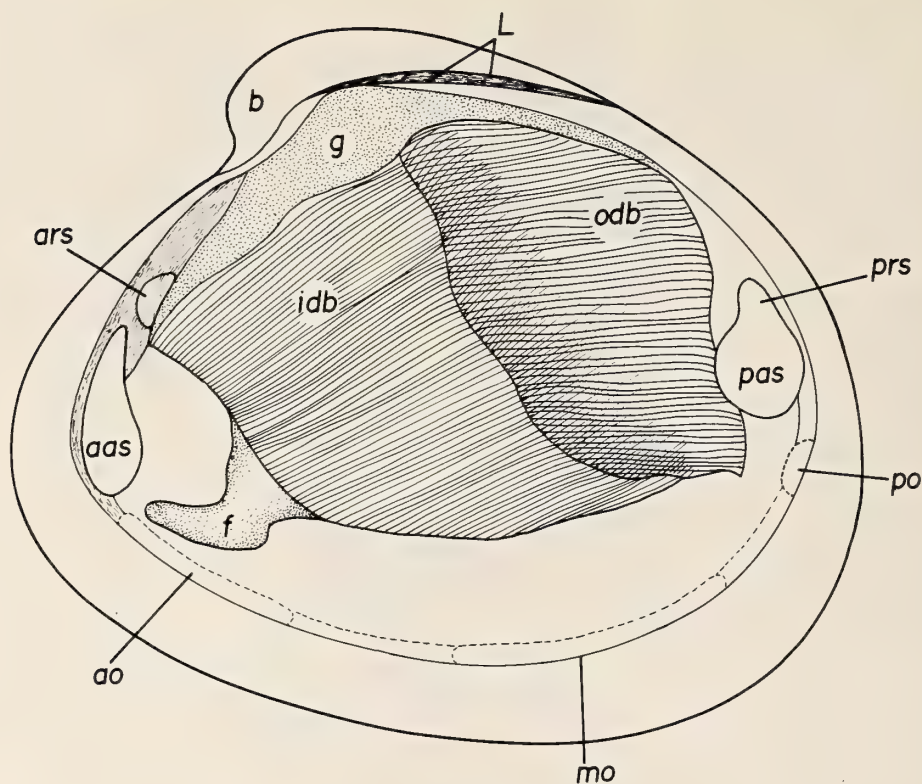


Figure 4

Gaimardia bahamondei Osorio & Arnaud, spec. nov., with left valve removed. aas, anterior adductor scar; ao, anterior (or pedal) opening; ars, anterior retractor scar; b, beak; f, foot; g, gonad; idb, gill inner demibranch; L, ligament; mo, median (or branchial) opening; odb, gill outer demibranch; pas, posterior adductor scar; po, posterior (or anal) opening; prs, posterior retractor scar.

to the description, this is neither *G. adamsiorum* nom. nov., nor *G. bahamondei* spec. nov.

Other related species, originally described in the genus *Modiolarca*, are *G. mesembrina* (Melvill & Standen, 1907)

and its synonym *M. picturata* Cooper & Preston, 1910; *M. gemma* Cooper & Preston, 1910; and *M. bennetti* Preston, 1913. The taxonomic status of these species is unclear; there are probably some other synonyms among them, and some will probably have to be referred to *Kidderia* Dall, 1886 (in the subfamily Cyamiinae of the family Cyamiidae *sensu* PONDER, 1971) instead of *Gaimardia*. We disagree with BERNARD (1983) who lists the first three names as additional synonyms of *G. trapesina*. In any event, we consider that the elongate shape, the color, and the hinges (when they are known) distinguish these species sufficiently from our Chilean material.

Finally, *G. kerguelensis* (Smith, 1885), known only from the type locality (Kerguelen Islands, south Indian Ocean), also has a very different elongate shape, and other characters showing no close affinities with the material from Isla Santa Maria.

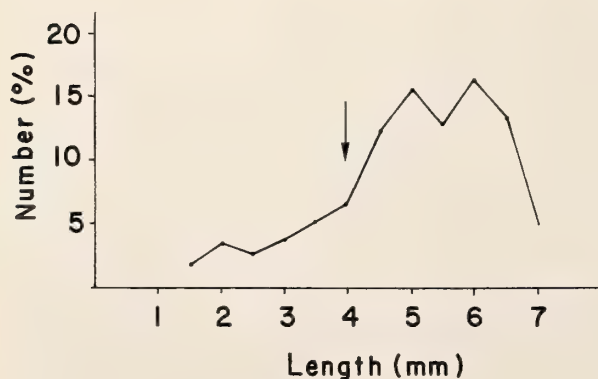


Figure 5

Gaimardia bahamondei Osorio & Arnaud, spec. nov. Population structure according to size (arrow indicates minimum size at maturity).

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Egg Masses and Larvae of Three Species of *Cerithium* from the Arabian Sea

by

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Abstract. An illustrated account of breeding habits and early larval development of three species of *Cerithium* from the coast of Karachi, northern Arabian Sea is given for the first time. *Cerithium morus* was studied earlier from tropical waters; however, the habits and development of the other two species, *C. sinensis* and *Cerithium* sp., are described here for the first time. *Cerithium morus* and *C. sinensis* deposit egg strings from which veligers hatch, whereas *Cerithium* sp. is ovoviviparous.

INTRODUCTION

THE BREEDING HABITS and larval development of gastropods of the genus *Cerithium* have only occasionally been studied. This work has been done on species found in the north Atlantic and Pacific Oceans by the following workers: LEBOUR, 1945; OSTERGAARD, 1950; FRETTER & GRAHAM, 1962; DAVIS, 1967; WOLFSON, 1969; D'ASARO, 1970; HOUBRICK, 1971, 1973; and CANNON, 1975. NATARAJAN (1957) has described the egg masses of *C. morus* from the Indian Ocean, and LO BIANCO (1888, in HOUBRICK, 1973) studied the egg mass of *C. vulgatum* from the Mediterranean Sea. Members of the family Cerithiidae are fairly abundant on the rocky beaches near Karachi, Pakistan. The present paper describes the breeding habits and early larval development of three species of *Cerithium* from this coast.

MATERIALS AND METHODS

Specimens of three species of *Cerithium* were collected from the rocky beaches at Manora and Buleji (see BARKATI & AHMED, 1983, for ecological notes on these beaches) in the Karachi area. Collections were made at regular biweekly intervals from July 1976 to June 1977. After each collection, specimens were placed for spawning in 1600-mL finger bowls in which water was changed daily and aerated continuously. The temperature of seawater in the bowls in the laboratory ranged from 28 to 31°C. All three species spawned to one extent or another in the laboratory. A microscopic study was also made of the larvae and juveniles that hatched from the egg masses or from individuals. Dimensions of the shells of the developing larvae were measured with an oculomicrometer, and illustrations were prepared with a camera lucida.

OBSERVATIONS

Breeding Season

Cerithium sinensis occurs fairly commonly on the rocky coast at Buleji (near Karachi) near the low-water mark, at a tidal height of about +0.15 to 0.3 m; at this level the snails are exposed only at very low tides. In the laboratory, specimens of this species deposited egg masses on the following dates: June 20, July 3, October 26, 29 and 31, November 1 and 11 in 1976, and July 25, 1977. In addition, two egg masses of this species were collected from the rocky beach at Paradise Point and Buleji on December 7 and 20, 1976.

Cerithium morus occurs on the same rocky beach (at Buleji) as *C. sinensis* but higher up at a tidal height of about 0.9 to 1.5 m. It is one of the most abundant species of gastropods on the open rocky coast of Karachi. Specimens of this species deposited egg masses in the laboratory on the following dates during the year 1976: June 7, September 4, October 19, 22, 30, and 31, and November 1. Altogether, 10 specimens which had been collected from Buleji and Manora spawned in the laboratory.

Cerithium sp. also occurs in the mid-tidal zone of the rocky beaches at Manora and Buleji, but it is less abundant than *C. sinensis* and *C. morus*. This species remains unidentified so far; however, voucher specimens of this species have been retained at the Institute of Marine Biology, University of Karachi, for future studies. In the laboratory, *Cerithium* sp. liberated a few juveniles on October 14.

No spawning occurred in months, other than those indicated, although specimens of all three species were examined for spawning throughout the year.

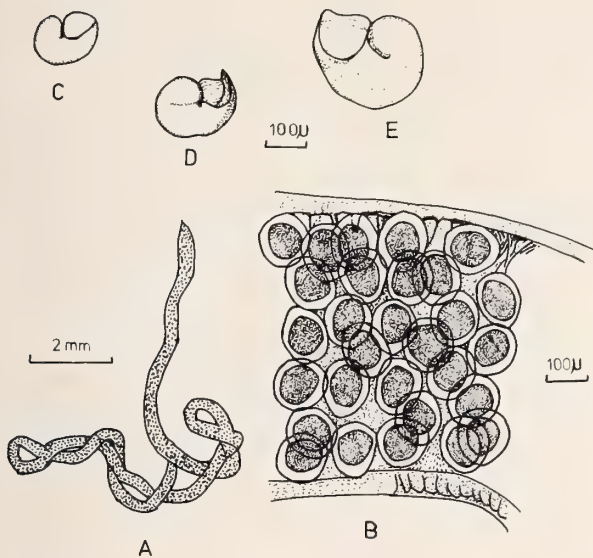


Figure 1

Cerithium sinensis: A. top view of an egg mass; B. portion of an egg mass enlarged; C. ventral view of newly hatched larval shell; D. ventral view of 24-h veliger shell; E. dorsal view of 48-h larval shell.

Egg Masses

Cerithium sinensis: The spawn of *C. sinensis* is described here for the first time. However, NATARAJAN (1957) earlier reported the spawn of an unidentified species of *Cerithium* from the Gulf of Manaar (India) that closely resembles the present egg mass.

Table 1

Dimensions of eggs and larval shells of *Cerithium sinensis* and *C. morus* at various stages of development. The values in the table are means \pm 1 standard deviation, followed by the number of observations in parentheses.

	<i>Cerithium sinensis</i>	<i>Cerithium morus</i>
Egg diameter (μ m)	94 \pm 6.75 (19)	99 \pm 5.49 (16)
Incubation period (days)	4–5 \pm 0.49 (7)	3–4 \pm 0.55 (5)
No. eggs/mass	5438	10,490
Larval shell height at hatching (μ m)	160 \pm 10.5 (25)	132 \pm 8.45 (18)
Larval shell width at hatching (μ m)	120 \pm 5.88 (25)	113 \pm 9.10 (18)
Larval shell height after 48 h (μ m)	187 \pm 4.99 (18)	176 \pm 5.47 (16)
Larval shell width after 48 h (μ m)	149 \pm 5.93 (18)	145 \pm 11.11 (16)
Larval shell height after 13 days (μ m)	—	246 \pm 13.03 (5)
Larval shell width after 13 days (μ m)	—	219 \pm 9.56 (5)

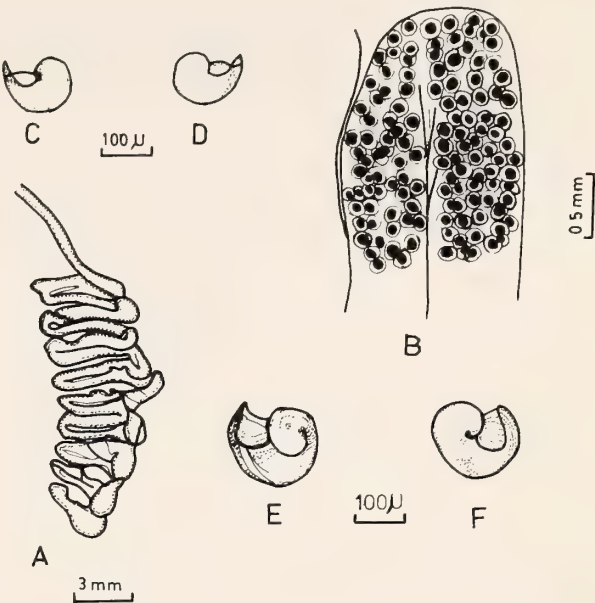


Figure 2

Cerithium morus: A. top view of an egg mass; B. portion of an egg mass enlarged; C and D. dorsal and ventral views of larval shells just after hatching; E and F. dorsal and ventral views of 48-h larval shells.

Deposition of egg masses of *C. sinensis* occurred at night. In the morning, laying of the egg masses was found to have been completed, indicating that these were deposited without interruption. They were usually deposited on the bottom of the containers. The two egg masses that were obtained from the field were collected from the sandy layer covering the surface of rocks.

The spawn of *C. sinensis* (Figure 1A) consisted of loosely coiled, or straight, long thin white tube-like strings. The strings measured on an average 1 mm wide and 67 mm long (SD = 15.28, N = 5). Free-swimming veligers hatched from these egg masses 4–5 days after their deposition. Dimensions of eggs and larvae at various stages of development are given in Table 1. At hatching the outer lip of the larval shell was extended in the middle and became more pronounced as the shell grew.

Cerithium morus: The spawn of *C. morus* was earlier described by NATARAJAN (1957) from the Gulf of Manaar (India).

In the present study the egg masses of *C. morus* were found to be deposited at night on the side walls of the glass bowls and only occasionally (in one out of ten cases) on the bottom. At spawning, the egg masses consisted of a narrow transparent, colorless, gelatinous tube, 0.5 mm wide and 92–196 mm long (SD = 35.22, N = 7), forming several coils compactly arranged and touching each other at several points. In one case the spawned mass covered

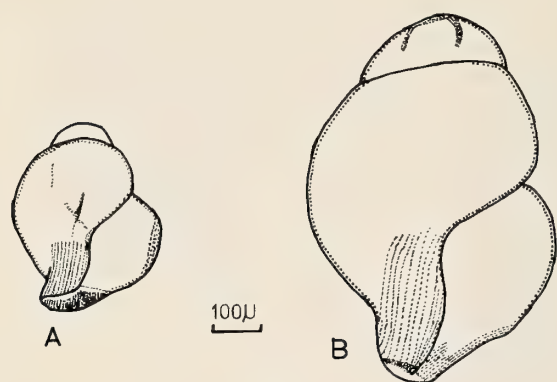


Figure 3

Cerithium sp. A. Larval shell 24 h after hatching; B. larval shell 96 h after hatching.

an area 25–36 mm long and 5–7 mm wide. The eggs were contained in egg capsules which were embedded in the gelatinous material of the egg mass. The eggs were more-or-less spherical, and so were the individual egg capsules (Figure 2B).

Larvae hatched from the capsules as free-swimming veligers (Figure 2C). At room temperature, which ranged from 28 to 31.5°C with an average of 30.2°C (SD = 0.92), the incubation period was 3–4 days but extended to 8 days in some cases. At hatching the larvae possessed transparent sculptureless shells. Subsequently, their outer lips formed a beaklike structure and developed a few striations; the umbilicus became more distinct. They survived in the laboratory for 15 days without food. At this stage their shells became thick and vertical striations became prominent.

Cerithium sp.: Five miniature snails of this species were found swimming actively in the finger bowls on the morning of October 14, 1976. The bowls were searched carefully for egg capsules, but none were found. Evidently, these juveniles had been extruded at night by the specimens placed for spawning. This species, therefore, seems to be ovoviviparous and its larvae seem to have direct development. The juveniles resembled the adults in the shape of their shells, which in both had a projected and recurved siphonal canal. The juvenile shells had translucent thick walls and were composed of two and a half whorls (Figure 3A). They survived in the laboratory for four days without food, and measured 798 µm high and 599 µm wide (Figure 3B). They were preserved alive after four days for future study. By this time, axial ribs started appearing on the projected siphonal canal.

DISCUSSION

Cerithium sinensis and *C. morus* spawn on the coast of Karachi during the monsoon and postmonsoon season from June to December. The single instance of spawning observed in the unidentified species of *Cerithium* from Ka-

rachi (in October) indicates that it also spawned during the postmonsoon season. On this coast the gastropod *Planaxis sulcatus* was found to breed from January to August (BARKATI & AHMED, 1982) and four species of *Thais* in spring and summer (BARKATI & AHMED, 1983). AHMED (1980) has categorized the marine organisms of the coast of Pakistan from the standpoint of their spawning seasons, as monsoon, winter-spring, spring-summer, and year-round spawners. The three species of *Cerithium* do not seem to fit this scheme. Knowledge of the spawning of these species, however, is based mostly on the deposition of egg masses in the laboratory, and may not truly reflect the situation prevailing in the field. The spawning season of *C. sinensis*, which occurs very low in the intertidal zone, might be expected to extend to the winter and spring months, or even throughout the year. This would conform with the conclusion, drawn by AHMED in his recent review (1980), that marine organisms of the coast of Pakistan (a subtropical coast) that occur close to the low tide mark or subtidally have a tendency to spawn in the winter and spring months and in some cases throughout the year.

The nature of the larval development of the three species needs further consideration. It is known that indirect development is the usual method of reproduction in members of the genus *Cerithium* compared to direct development, which has so far been reported from only two species, namely *C. muscarum* and *C. variabile* (HOUBRICK, 1973). The three species of *Cerithium* reported herein can be placed in two groups according to their mode of development. In the first type, the egg mass consists of filaments containing egg capsules from which free-swimming larvae hatch, as in *C. sinensis* and *C. morus*. The second type is represented by *Cerithium* sp. in which miniature snails hatch directly from the parent. In this case, juvenile snails settled on the bottom after only a brief period of swimming. Although this is the first time a species of *Cerithium* has been found to possess viviparous development, this mode of development is not new to the present environment: another prosobranch, *Planaxis sulcatus*, has recently been shown to be viviparous. Thus, the observations made during the present study show that, in addition to the usual method in which gelatinous filaments containing egg capsules are produced, extrusion of juveniles from the mother snails may also occur.

The number of eggs per spawn has been described earlier for a number of species of *Cerithium* (see HOUBRICK, 1973). This ranges from 8800 in *C. literatum* to 90,000 in *C. auricoma*. The spawns of *C. morus* and *C. sinensis* were found in the present study to contain an average of 10,490 and 5438 eggs, respectively. The number of eggs per spawn in *C. sinensis*, therefore, is the lowest of all the *Cerithium* species studied so far.

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Male Reproductive System of *Chorus giganteus* (Lesson, 1829) (Muricidae: Prosobranchia): Anatomical and Histological Description

by

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Abstract. The male reproductive system of *Chorus giganteus* is anatomically and histologically described. This system is formed by a testis, seminal vesicle, posterior deferent duct, prostate, anterior deferent duct, and penis. Besides the germ cells, the occurrence of some large cells inside the seminiferous tubules is reported; these cells may play a role similar to that of nurse cells. Also, polynucleated cellular masses are observed corresponding to gonial cells with incomplete cytokinesis. At the posterior end of the prostate, the lumen of the gland is connected with the mantle cavity by means of a duct, which, toward the anterior zones, is replaced by a double sheet of epithelium-like cells corresponding to the so-called line of fusion of the open system from less-advanced forms. The line of fusion extends from the duct, connecting with the mantle cavity at the posterior limit of the prostate, along the entire length of the male duct to the penis.

INTRODUCTION

THE FAMILY MURICIDAE has a wide geographical distribution. Previous studies have revealed the existence of similarities in the anatomical and histological organization of the reproductive system not only among the species of this family (FRETTER & GRAHAM, 1962, in WEST, 1979; PURCHON, 1977; HYMAN, 1967), but also among those of the neogastropod families Buccinidae (WEST, 1979), Columbellidae (HOUSTON, 1976), and others.

Chorus giganteus (Lesson, 1829) is a muricid living on sandy and muddy sea bottoms, 8-30 m deep (LÉPEZ, 1981). Its geographical distribution extends from Antofagasta (23°40'S; 70°25'W) through Valdivia (39°55'S; 73°10'W), Chile (OSORIO, 1979).

Since *Chorus giganteus* is an edible snail that has recently acquired economical importance, studies on different aspects of the reproductive biology have been initiated. In the last two years, studies have been done on the reproductive cycle (LÉPEZ, 1981), the intracapsular development of eggs and larvae (GALLARDO, 1981), and fecundity (OLAVE, 1981) of this species. In the present paper an anatomico-histological study of the male reproductive system is reported.

MATERIALS AND METHODS

Sexually mature individuals were collected at Burca (36°28'S; 75°55'W), Concepción, Chile, by scuba diving

and maintained in running seawater aquaria at the Marine Biology Station of the University of Concepción. Anatomical descriptions were made from live specimens and 10% formalin-fixed material.

For the histological study, tissues were excised from freshly dissected animals and fixed for a minimum of 24 h in 10% formalin. Following fixation, tissues were dehydrated through a graded series of ethanol and embedded in paraffin (Merck 56-58°C).

Serial sections 5-6 μ m thick were cut and mounted on albuminized slides.

The following stains were used: (1) Hematoxylin-Phloxine (HUMASON, 1967), (2) Heidenhain's iron-haematoxylin (HUMASON, 1967), (3) PAS with amylase control (LILLIE, 1965), (4) Feulgen reaction (LILLIE, 1965), and (5) Methyl Green-Pyronine (LILLIE, 1965).

RESULTS

Anatomy

The male reproductive system of *Chorus giganteus* is formed by a single testis, seminal vesicle, posterior deferent duct, prostate, anterior deferent duct, and penis (Figures 1, 2).

Testis

The testis (Figures 1, 2) of a sexually mature male is a single mass located in the last whorls of the shell. The

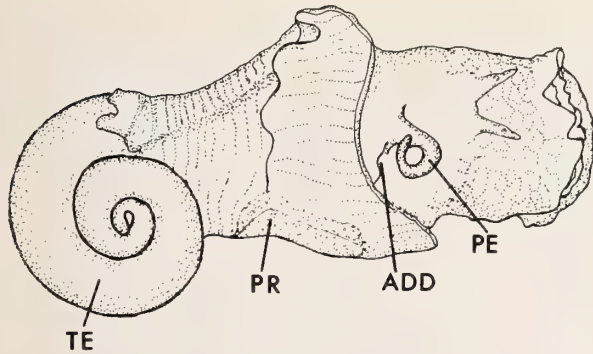


Figure 1

Male *Chorus giganteus*. Whole specimen with shell removed. TE, testis; PR, prostate; ADD, anterior deferent duct; PE, penis.

testis adheres to the dorsal side of the digestive gland along its total length. No clear separation is observed with respect to the digestive gland because the efferent ductuli of the testis slightly intrude between the tubules of the glandular mass. The testis color varies from dark brown to light yellow depending on the stage of gonad development.

The efferent ductuli join to form a single spermatic duct (Figure 2) that leaves the testis and then passes superficially along the columellar side of the visceral mass.

Seminal vesicle

After leaving the testis, the spermatic duct becomes convoluted constituting a seminal vesicle (Figure 2), which measures 3–4 mm in length. The seminal vesicle is filled with spermatozoa.

Posterior deferent duct

Following the seminal vesicle, the spermatic duct (Figure 2), which lies laterally to the visceral mass in the inner side of the whorls, straightens and passes between the heart and kidney.

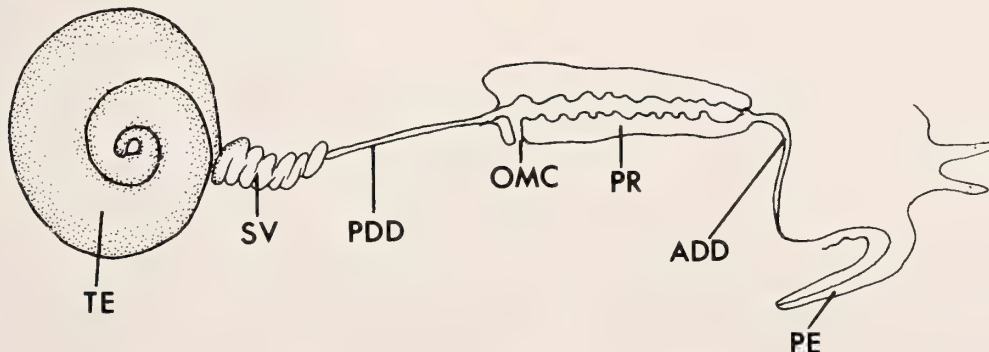


Figure 2

Male reproductive system. TE, testis; SV, seminal vesicle; PDD, posterior deferent duct; OMC, opening to the mantle cavity; PR, prostate; ADD, anterior deferent duct; PE, penis.

Prostate

The posterior deferent duct extends into the prostate (Figure 2), which is located along the right side of the roof of the mantle cavity (Figures 1, 2). The prostate, which encloses the spermatic duct, is a glandular mass about 30 mm long, depending on the developmental stage of the specimen.

Anterior deferent duct

After leaving the prostate, the spermatic duct, referred to as the anterior deferent duct (Figure 2), goes straight down to the floor of the mantle cavity. Once on the floor of the mantle cavity, the duct extends a small distance along the mantle cavity laterally, following the curvature of the cavity, and then running anteriorly to the penis along the body wall. The course of the anterior deferent duct runs mainly on the surface of the floor of the mantle cavity (Figure 1).

Penis

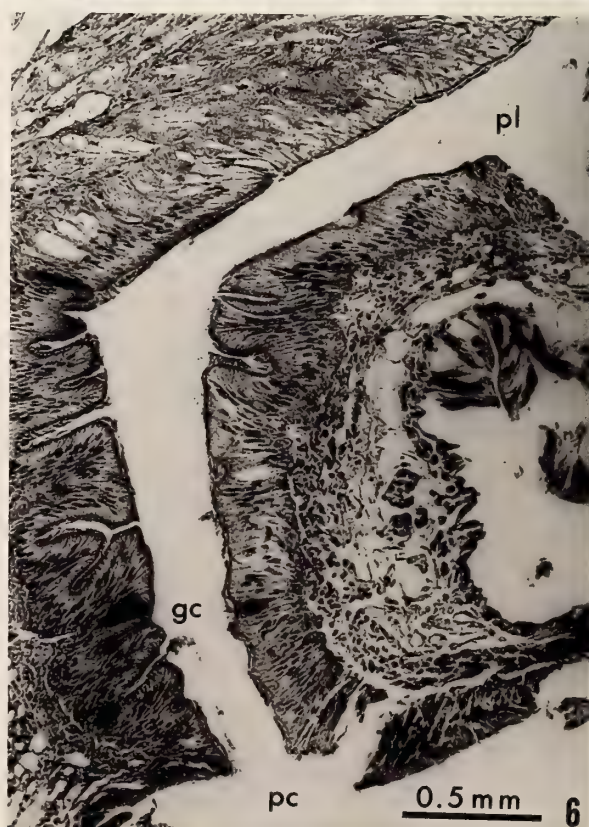
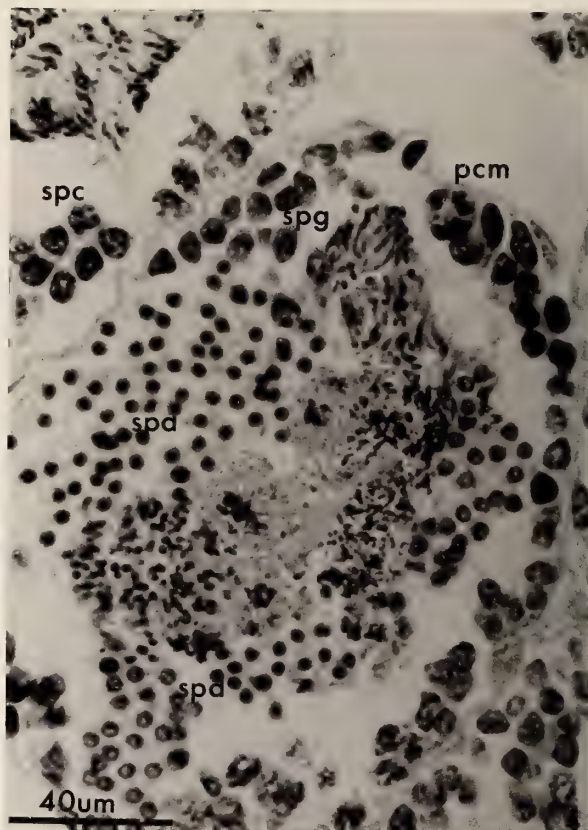
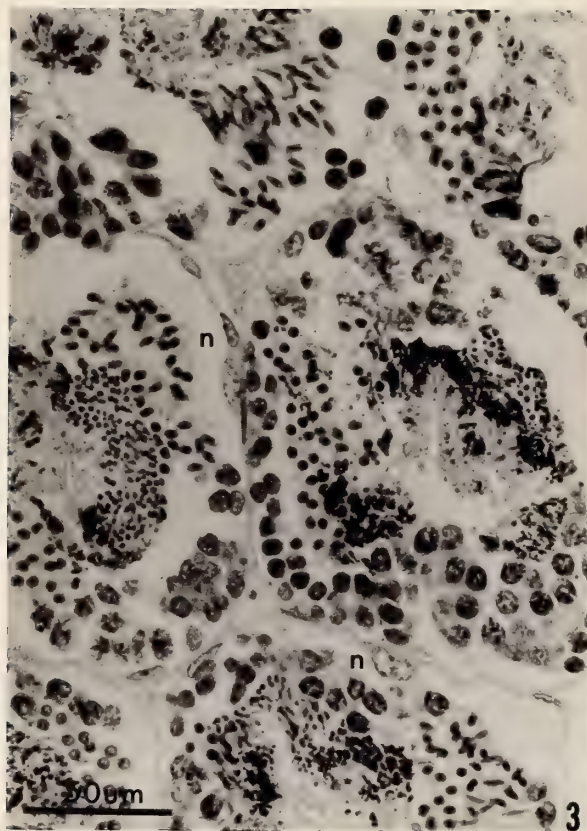
This organ is compact, with a wide base and a fusiform distal end (Figures 1, 2). It is dorso-ventrally flattened and situated behind and at the right side of the tentacles. Average length is about 20 mm.

Histology

Testis

The testis, together with the digestive gland, is covered by the pallial epithelium, which is a simple cuboidal type. The cells of the epithelium have round basal nuclei. Sub-jacent to the pallial epithelium is a thin albuginea.

The testis is composed of many convoluted seminiferous tubules with an average diameter of 130 μm (Figure 3). Each tubule is externally delimited by a thin adventitium. The germinal epithelium underlying the external adventitia is composed of spermatogenic cells clustered in groups; all cells in a group are in the same maturation phase.



Among the basal germ cells, and resting on the adventitia, there are a few larger cells each with a less densely staining nucleus; no nitid cell limits are observed.

Germ cells

- (a) *Spermatogonia*: These are round cells with a large homogeneous, deeply staining nucleus, and scanty cytoplasm. They lie adjacent to the basal lamina on the luminal side of the germinal epithelium.
- (b) *Primary spermatocytes*: Spermatocytes and spermatogonia are of the same size, but the nucleus of the former is more delimited and laterally located, with groups of meiotic chromosomes. Secondary spermatocytes are indistinguishable from primary spermatocytes.
- (c) *Spermatids*: Early spermatids are small, rounded cells with a central, spherical, homogeneous nucleus and scanty cytoplasm. The morphology of these cells varies during spermiogenesis and they tend to be elongate.
- (d) *Spermatozoa*: These are slender fusiform cells with a total length of 98.75 μm . The head, 57.19 μm long, is pointed and slightly wider than the tail.

The seminiferous tubules occasionally contain polynucleated masses corresponding to gonias with incomplete cytokinesis (Figure 4).

Seminal vesicle

The convoluted portion of the spermatic duct, the seminal vesicle, is lined with a simple cuboidal ciliated epithelium. The epithelial cells contain a lightly staining cytoplasm, a large oval central nucleus, and very long cilia (30 μm). Beneath the epithelium and between the loops of the duct, dense connective tissue and free blood cells are seen. At the distal end, the seminal vesicle has a sphincter with abundant muscle fibres interspersed with the connective tissue surrounding the epithelium.

Posterior deferent duct

The posterior deferent duct is internally lined with a simple cuboidal ciliated epithelium resembling that of the seminal vesicles, but in this portion of the spermatic duct the epithelium greatly invaginates and no spermatozoa are

seen in the lumen. Beneath the epithelium a thin PAS-positive line is observed. The cuboidal epithelium is externally surrounded by dense connective tissue with a few intermingled muscle fibres and spaces with blood cells.

Prostate

The prostate is a glandular differentiation of the wall of the deferent duct which greatly evaginates toward the lumen (Figure 5). The gland is delimited internally by a simple ciliated columnar epithelium, although in some zones the epithelial cells increase in height and intrude into the underlying glandular mass. The cytoplasm of the epithelial cells contains fine granules which stain with Phloxine, and larger PAS-positive granules. The nuclei of the epithelial cells are located in a basal position and their shape varies from spherical to fusiform. The cilia are shorter (14–15 μm) than those of the posterior deferent duct. Goblet cells intermingle with the epithelial cells.

Underlying the epithelium is the glandular tissue, which is composed of a mass of secretory cells arranged in radially branched tubules converging towards the prostate lumen. The secretory tubules are separated by thin septa of connective tissue. The glandular cells close to the ciliated epithelium show a great amount of secretory material gradually decreasing toward the outer limit of the prostate. In this area the cytoplasm of the secretory cells is dominated by large vacuoles displacing the nucleus to the periphery of the cell. The nucleus is large and spherical, and contains granular and loose chromatin.

Externally surrounding the glandular zone, loose connective tissue with fibres concentrically arranged around the prostate is observed.

At the posterior end of the prostate, the lumen of the gland is connected with the pallial cavity by a small duct (Figure 6). This duct is about 124 μm in diameter and 1.116 mm in length. It is lined with a pseudo-stratified ciliated columnar epithelium containing fusiform nuclei. The goblet cells of the epithelium are filled with granules that stain deeply with Phloxine.

In serial sections toward the anterior end of the prostate, the duct connecting the lumen and the pallial cavity no longer is observed; instead, a double sheet of epithelium-like cells runs all the way along the gland. This double sheet of epithelium-like cells is immersed in the connective tissue surrounding the prostate (Figure 7).

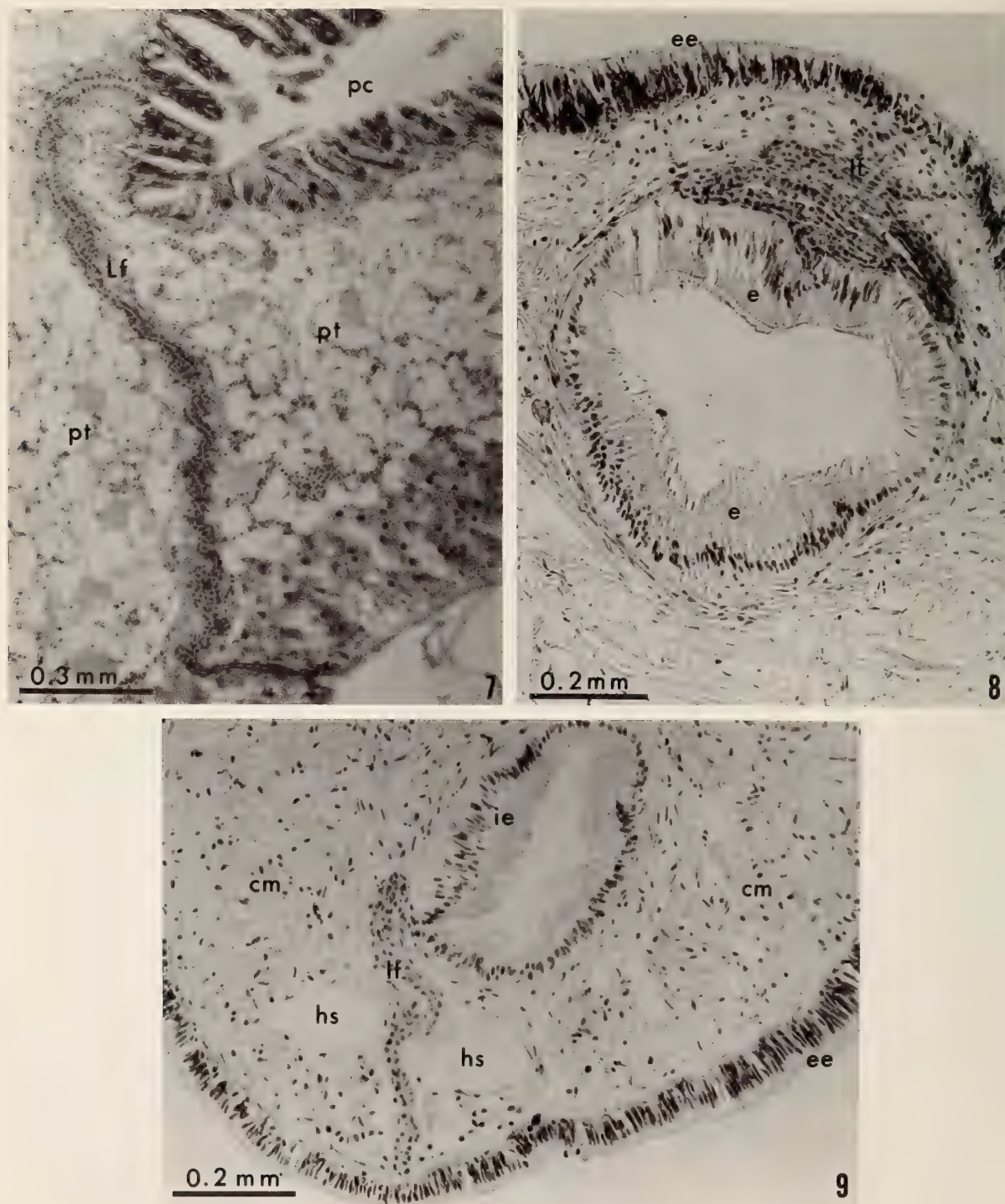
Explanation of Figures 3 to 6

Figure 3. Cross-section of testis showing seminiferous tubules. n, nucleus of large cell with no clear cytoplasmic limits.

Figure 4. Seminiferous tubule showing germ cells clustered in groups in the same maturation phase. spg, spermatogonia; spc, spermatocytes; spd, spermatids; pcm, polynucleated cellular masses.

Figure 5. Section of prostate. ie, inner ciliated columnar epithelium; gt, glandular tissue; pl, prostatic lumen.

Figure 6. Duct connecting the lumen of the prostate with the pallial cavity. gc, goblet cells of the epithelium filled with granules deeply stained with Phloxine; pl, prostatic lumen; pc, pallial cavity.



Explanation of Figures 7 to 9

Figure 7. Double sheet of epithelium-like cells (line of fusion). pt, prostatic tissue; pc, pallial cavity.

Figure 8. Cross-section of anterior deferent duct. e, simple ciliated columnar epithelium; lf, line of fusion; ee, external epithelium.

Figure 9. Cross-section of penis showing the spermatic duct. ie, inner epithelium; cm, network of connective tissue and muscle fibres oriented in all directions; lf, line of fusion; hs, haemal spaces; ee, external epithelium.

Anterior deferent duct

The anterior deferent duct is internally lined with a simple ciliated columnar epithelium, only slightly invaginated (Figure 8). The cytoplasm of the epithelial cells is granular in the basal portion of the cell and homogeneous in the apical end; nuclei are small, spherical and centrally located. The epithelium is underlain by a thin layer of connective tissue.

All along the length of the duct the double sheet of epithelium-like cells is observed (Figure 8), which, as it has been previously described for the prostate, also connects the lumen of the duct with the pallial cavity.

Penis

The penial duct is a straight tube, located laterally within the organ and internally coated by a simple ciliated columnar epithelium of various heights (Figure 9). The cytoplasm of the epithelial cells is homogeneous; nuclei are oval in shape, basally located, and contain dense granular chromatin. Goblet cells are seen between epithelial cells.

The penial duct is surrounded by a mass of tissue composed of a circular muscle layer adhered to the inner epithelium, and a complex network of connective tissue. Muscle fibres oriented in all directions, small haemal spaces, and bundles of nerve fibres intermingle with the network of connective tissue. Each bundle of nerve fibres is enveloped by a thin layer of connective tissue. All of these tissues provide the penis with a compact structure. The surface of the penis is coated by a simple ciliated columnar epithelium. The cytoplasm of the columnar cells is homogeneous, but it is visible only in the apical end, because the rest of the cell is entirely occupied by a large fusiform nucleus. Goblet cells are also seen between the epithelial cells. Also, small basal cells with spherical nuclei are observed interspersed with epithelial cells.

All along the penis, and always connecting the spermatid duct with the external epithelium, the double sheet of epithelium-like cells (Figure 9), previously described for the prostate and the anterior deferent duct, can be observed again.

The whole structure of the penis exhibits basically the same histological pattern just described, but the proximal region of this organ shows a greater abundance of muscle tissue, gradually decreasing toward the tip of the penis where connective tissue predominates. The number of goblet cells in the surface epithelium gradually decreases from the basal zone to the apical end.

DISCUSSION

The male reproductive system of *Chorus giganteus* does not differ from the general pattern described by HOUSTON (1976), HYMAN (1967), and PURCHON (1977) for the most-evolved neogastropods. It consists of a testis, seminal ves-

icle, posterior deferent duct, prostate, anterior deferent duct, and penis.

In addition to the germ cells, the seminiferous tubules contain some larger cells, not clearly delimited, that would correspond to the basal cells in *Colus stimpsoni* (Mörch, 1867) as described by WEST (1978). These cells may play a nursing role for the differentiation of the germ cells.

Large polynucleated cells, corresponding to gonias that do not complete cytokinesis during cell divisions, can also be observed within the seminiferous tubules. This phenomenon was not observed in *Concholepas concholepas* (Bruguiere, 1789) (GUZMÁN *et al.*, 1972), but it was reported for *Colus stimpsoni* by WEST (1978).

The first portion of the posterior deferent duct is the seminal vesicle, which ends in a sphincter muscle. The occurrence of a seminal vesicle is not a feature common to all muricids, since in *Acanthina angelica* I. Oldroyd, 1918, *Trophon truncatus* (Strom, 1768), and some representatives of the genus *Thais*, the seminal vesicle is absent (HOUSTON, 1976). However, this structure is found in *Concholepas concholepas* (GUZMÁN *et al.*, 1972), *Trophon barvicensis* (Johnston, 1825), *Ceratostoma foliatum* (Gmelin, 1791) and *Urosalpinx cinerea* (Say, 1822) (HOUSTON, 1976).

In *Chorus giganteus*, a segment of the wall of the spermatid duct is modified so as to form the prostate, whose glandular tissue forms a compact mass around the lumen of the duct; the secretion products are directly poured into the lumen of the duct. This histological pattern differs from that of *Concholepas concholepas* because, in spite of the fact that in *C. concholepas* a distinct prostatic gland occurs, the histology of this gland reveals isolated glandular acini immersed in connective tissue, each one having its own duct that opens into the spermatid duct (GUZMÁN *et al.*, 1972).

The small, ciliated duct connecting the gland lumen with the pallial cavity acts in *Chorus giganteus* as an escape outlet for spermatozoa in case copulation is disturbed by external factors. Although this arrangement is present in many higher mesogastropods and neogastropods (PURCHON, 1977), in *Concholepas concholepas*, a Chilean species of the same family and similar geographical distribution, this connection has not been reported (GUZMÁN *et al.*, 1972).

In the anterior portion of the prostate of *Chorus giganteus*, the small duct is replaced by a double sheet of epithelium-like cells running along the prostate, the anterior deferent duct, and the penis. This sheet is also found in *Acanthina*, *Mitrella*, and species of related families, and it corresponds to the so-called line of fusion of the open system from less-advanced species. The open system is found in several species of *Littorina*, in which the prostate is composed of two glandular lobes and remains open throughout its entire length (HOUSTON, 1976).

In *Chorus giganteus* the penial duct is straight, as in other genera of the same family, and it is different from

that of *Concholepas concholepas* (GUZMÁN *et al.*, 1972) and that of some species of *Thais*, *Trophon*, and *Ocenebra* (HOUSTON, 1976) in which the penial duct has been described as highly convoluted. Finally, the penial duct is laterally located within the penis in *Chorus giganteus*, whereas in *Concholepas concholepas* (GUZMÁN *et al.*, 1972) and in *Columbella fuscata* Sowerby, 1832 (HOUSTON, 1976) it is centrally positioned.

ACKNOWLEDGMENTS

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Anesthetic Methods for the Moon Snail *Polinices lewisii*

by

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Abstract. Nine chemicals and hypothermia were tested on the moon snail *Polinices lewisii* for their effectiveness as anesthetics. Hypothermia and five of the drugs induced anesthesia. Althesin, a mixture of the steroids alphaxalone and alphadolone acetate, appeared to be the most desirable anesthetic. Hypothermia and xylazine can also be recommended for routine use. Less favored were ethanol and sodium pentobarbital. Benzyl alcohol was the most lethal of the compounds tested.

INTRODUCTION

SUCCESSFUL SURGERY, a central requirement for many physiological studies, often depends on an effective method of anesthesia. Although anesthetic procedures are well established for vertebrates, particularly mammals (GILMAN *et al.*, 1980), this is not the case with invertebrates despite the use of invertebrate preparations in studying the neuronal and synaptic activity of many mammalian anesthetics (JUDGE, 1980). In the mollusks only a few attempts have been made to systematically evaluate the effectiveness of anesthetic procedures (*e.g.*, ANDREWS & TANSEY, 1981 for a cephalopod; RUNHAM *et al.*, 1965, for several gastropods). Although RUNHAM *et al.* (1965) found several agents to be effective anesthetics, most of these suffered the drawback of exceedingly long induction times. This study, an attempt to update the RUNHAM *et al.* (1965) investigation, details the search for an effective, quick-acting anesthetic for the moon snail *Polinices lewisii* (Gould, 1847).

MATERIALS AND METHODS

The moon snails used in this study ranged in wet weight from 75 to 160 g; animals were weighed in the retracted state. All animals, collected in Barkley Sound, Vancouver Island, were held for at least five days in running seawater at 31 to 32‰ salinity and 10 to 12°C before experimentation was commenced. The holding tank was provided with a fine sandy bottom.

The anesthetic methods tried can be divided into two

categories: physical and chemical. In the physical method, hypothermia, an animal was placed in a seawater bath and the bath temperature dropped to 2°C over a one-hour period. In the chemical methods, the following agents were tried: Althesin (Galaxo Laboratories), benzyl alcohol, carbon dioxide, ethanol, magnesium chloride, MS 222 (Sigma), quinaldine, sodium pentobarbital (Somnotol-MTC Pharmaceuticals), and xylazine (Rompun-Cutter Laboratories). To obtain estimates of initial anesthetic concentrations, the following sources were consulted: BELL (1964), RUNHAM *et al.* (1965), and the manufacturers' literature.

At ambient seawater temperature, anesthesia with chemicals was conducted on an expanded animal placed in one liter of seawater in a glass dish of 20 cm diameter and 7 cm height. Liquid chemicals then were added slowly to the bath, with mixing accomplished by a peristaltic pump. Carbon dioxide simply was bubbled into the bath.

The behavior of an animal was visually monitored during the induction. Generally the signs noted were as follows: (1) hyperactivity, unusual crawling or extreme expansion of the foot and mantle; (2) retraction responses, either of the whole or parts of the animal; (3) lack of responsiveness to a water jet and touch of a stainless steel probe; and (4) flaccid expansion, especially of the tentacles.

If induction was successful the animal was allowed to recover in running seawater, after which the amount of anesthetic was calculated. Each chemical was given six individual animal trials; for the successful ones a second phase of testing occurred in an attempt to establish the minimum concentration needed. This was accomplished by testing at one half the initial concentration and then again at added 10% increments.

After establishing the minimum concentration, a new

¹ Requests for reprints should be sent to the University of Calgary address.

Table 1

Summary of anesthetic actions on the moon snail
Polinices lewisii.

Anesthetic	No. of animals	Concentration (%)	($\mu\text{g}/\text{mL}$)	Induction time (h)	% retracted during surgery ¹	% survived after 1 week ²
Althesin	18	0.15	14 ³	2	22	93
Benzyl alcohol	10	0.5–1	—	>1	0	10
Ethanol	15	4	—	3	47	75
Sodium pentobarbital	10	0.14	91	2.5	20	38
Xylazine	20	0.06	12	2.5	35	62
Cold (2°C)	8	—	—	1.5	50	100

¹ Surgery lasted 0.5 h.

² Retracted animals eliminated.

³ This is the final concentration of alphaxalone, one of two active ingredients in Althesin. The commercially available preparation of Althesin contains alphaxalone (9 mg/mL) and alphadolone acetate (3 mg/mL). The latter compound, although possessing some anesthetic activity in humans, is added to increase the solubility of the mixture (REYNOLDS & PRASAD, 1982).

batch of animals subjected to the successful anesthetics underwent surgery. This operation consisted of cutting a hole of 0.5-mm diameter in the dorsal part of the shell and another of 4-mm diameter in the left ventral part of the shell in order to implant impedance-conversion electrodes. A Biocom impedance converter coupled to a Gould recorder was used to make recordings of body movements during the early recovery phase; total recovery of these animals was monitored for at least one week.

RESULTS

For various reasons the following substances were rejected as anesthetics for moon snails: carbon dioxide (up to saturation), magnesium chloride (2.4%), MS 222 (1 mg/mL) and quinaldine (saturated solution). Carbon dioxide and magnesium chloride both failed to induce anesthesia within four hours. However, MS 222 and quinaldine appeared to be highly noxious and caused the moon snails to retract into the shell. Once retracted the moon snails did not extend while immersed in the solutions containing MS 222 and quinaldine.

All other chemicals and hypothermia induced varying states of anesthesia. Table 1 summarizes the results of the second-phase testing of those agents. Exactly when the effects of the agents wore off was difficult to ascertain; therefore, the percentage of animals that retracted during surgery was used as the comparative indicator of that factor.

The behavior of animals during recovery was variable and depended on the anesthetic used. Moon snails that were recovering from cold exposure and ethanol immersion remained quiet for one to two hours after being placed in running seawater, after which the animals tended to crawl around the recovery tank for several hours. However, with Althesin, benzyl alcohol, and xylazine, the quiescent period was more extensive and lasted as long as a day. During the longer quiescent periods many of the animals turned upside down, but this behavior was also observed in normal animals both in the wild and in captivity.

Impedance recordings of body movement within the shell revealed that the quiescent period masked other aspects of the recovery (Figure 1). In all instances body movements

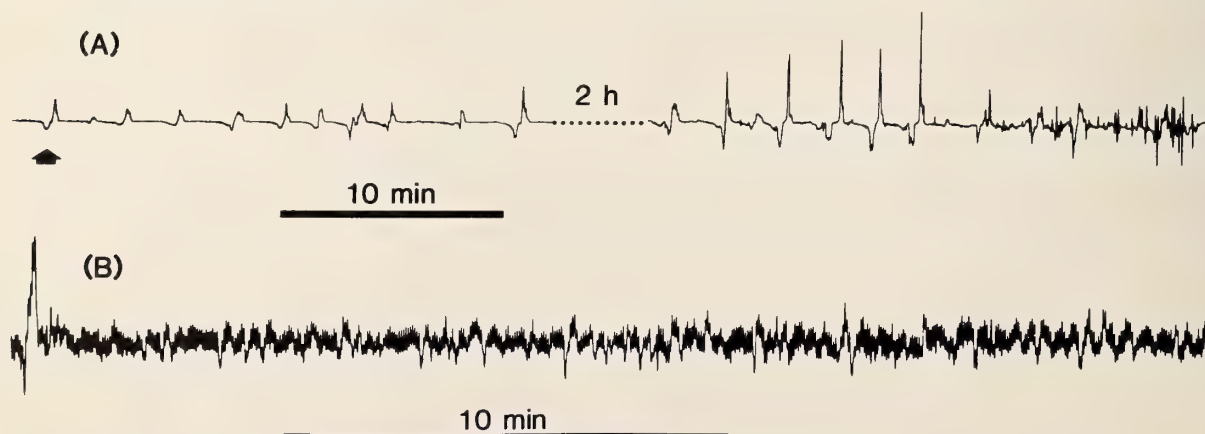


Figure 1

Impedance recording of body movements within the shell of a specimen of *Polinices lewisii* following Althesin anesthesia. (A): early recovery period—the arrow indicates the onset of the body movements, which in this instance occurred approximately 1.2 h after the animal was placed in running seawater to recover. (B): fully recovered animal—the recording was made while the animal was crawling and occurred 40.7 h after the animal was in running seawater. Unlike the previous recording (A), the predominant activity in (B) is the beating of the heart upon which is superimposed other body movements.

occurred within the shell with no apparent external body conformational changes. The earliest onset of these internal body movements followed cold exposure and Althesin immersion, with benzyl alcohol delaying the movements longest.

Table 1 also demonstrates that benzyl alcohol was the most lethal of the chemicals, inducing such visible signs of distress as the sloughing off of an animal's epidermis and pigment within two days. Deaths from the other agents gave no such outward indication.

DISCUSSION

The results of this study demonstrate that anesthesia of the moon snail *Polinices lewisii* can be accomplished by immersion in solutions of anesthetic agents. Because a primary requirement of the study was to ensure that animals remained expanded, no attempt was made to inject anesthetics. In this regard, there was also a practical consideration of finding a blood space within the voluminous aquiferous system, for BERNARD (1968) has shown that system to contain a volume of water equal to 50% of the total weight.

This study also revealed several well-known aquatic vertebrate anesthetics, carbon dioxide, MS 222, and quinaldine (BELL, 1964), to be ineffective for moon snails. For MS 222 and quinaldine the problem appeared to be their highly noxious nature, which caused animals to retract into the shell. However, rejection of carbon dioxide was based on its failure to induce anesthesia after four hours.

Like carbon dioxide, magnesium chloride was also rejected for its inability to cause anesthesia within a reasonable time. In the Mollusca, as in many invertebrates, magnesium chloride is most widely used as a narcotizing agent (RUNHAM *et al.*, 1965). Runham and his colleagues, employing magnesium chloride to anesthetize the marine prosobranchs *Littorina littorea* and *Nucella lapillus*, found that it took overnight to accomplish the task.

Hypothermia appears to be a reasonable means of anesthesia when the surgical procedures are simple. ANDREWS & TANSEY (1981) indicated that hypothermia is a desirable method in *Octopus*, especially for neuropharmacological experiments.

Of the several chemicals, Althesin appears to be the optimal agent for use in the moon snail. It possesses several acceptable characteristics: low lethality, comparatively short induction time, and relatively quick recovery time. Alphaxalone, the major active ingredient of Althesin, has been injected into the crabs *Carcinus maenas* and *Cancer pagurus* to bring about a "sleep time" of two to three hours (OSWALD, 1977). In the moon snail the "sleep time" fol-

lowing Althesin anesthesia appears to be similar to that of crabs subjected to alphaxalone.

Xylazine ranks as the second chemical of choice, possessing a higher lethality than Althesin. OSWALD (1977) found xylazine to be a desirable, fast-acting anesthetic for crabs.

Ethanol and sodium pentobarbital could be used, but have little to offer in preference to Althesin and xylazine. Obviously if cost and availability are factors, then ethanol can be considered. The lethal nature of benzyl alcohol makes it wholly undesirable as an anesthetic in moon snails.

No attempt was made in this study to elucidate the mode of action of any of the chemicals. It is tempting to speculate that the drugs Althesin and xylazine were exerting a central action. However, more study is needed to confirm this as well as to understand the site of entry, distribution, and breakdown of these drugs. Althesin and xylazine should be tested in other gastropod species to see whether they may serve as general anesthetics for snails.

ACKNOWLEDGMENTS

I thank Dr. R. E. Foreman, Director of the Bamfield Marine Station, and his staff for the many kindnesses shown during my stay at the station. In particular, extensive thanks go to Ms. Sabina Leader for help in collecting and maintaining animals. I also thank Dr. S. H. Roth for bringing Althesin to my attention.

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NOTES, INFORMATION & NEWS

An Earlier Name for *Nassarius corpulentus* (C. B. Adams, 1852)

by

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Examination of type specimens of Cancellariidae in the Muséum National d'Histoire Naturelle, Paris, has revealed that *Cancellaria nassiformis* Lesson, 1842:204, is not cancellariid but is the species later described as *Nassa corpulenta* C. B. Adams, 1852:284. The type lot of *Cancellaria nassiformis* Lesson consists of seven syntypes from Acapulco, Mexico, the only locality cited by Lesson.

As Lesson's name has ten years' priority over the one proposed by C. B. Adams, it must either be employed as the correct name or it must be rejected by action of the International Commission on Zoological Nomenclature. This note is being published to call this matter to the attention of systematists interested in the Panamic-Pacific Nassariidae who can better judge which course of action should be followed.

The writer is indebted to Dr. Philippe Bouchet, Curator of Marine Mollusks, Muséum National d'Histoire Naturelle, Paris, who not only made the type material available for study, but also provided bibliographic information. Appreciation is also expressed to Dr. James H. McLean, Los Angeles County Museum of Natural History, Los Angeles, for examining some of these syntypes and confirming their conspecificity with *Nassarius corpulentus* (C. B. Adams).

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least, wishes to avoid this possible financial handicap to the younger contributors. However, because of the high cost of halftone plates, a suitable contribution to reimburse the Society must be sought. Similarly, contributions will be sought from authors (or preferably their institutions) to help defray costs of line drawings and tables in excess of four simple ones. We emphasize, however, that requests for donations are totally unrelated to acceptance or rejection of manuscripts for The Veliger. Acceptance is entirely on the basis of merit of the manuscript. Donations are to be made *after* publication, if at all, and are strictly on a voluntary basis.

Nevertheless, donations by authors and readers are necessary for the continued good health of our Society, the stated aim of which is to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible. Authors and readers are reminded that contributions to the C.M.S., Inc. are deductible by donors as provided in section 170 of the Internal Revenue Code (for Federal income tax purposes).

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The California Malacozoological Society acknowledges with gratitude a very generous contribution to the Endowment Fund by the Drs. J and W. Gibson-Smith of the Universidad Central de Venezuela, Caracas, in appreciation of Dr. Rudolf Stohler's outstanding Editorship on the occasion of his retirement after 25 years. Such gifts contribute greatly to the continuation of The Veliger, a monument to the monumental efforts of Dr. Stohler.

American Malacological Union

The AMU will hold its 50th annual meeting in Norfolk, Virginia, July 22-27, 1984. The meeting promises to be of interest to serious amateurs as well as professionals. For further information, write Dr. Robert Robertson, President, Department of Malacology, Academy of Natural Sciences, 19th and the Parkway, Philadelphia, PA 19103.

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BOOKS, PERIODICALS & PAMPHLETS

Mollusca

by KENNETH J. BOSS. 1982. Pp. 945-1166 in Vol. 1 and pp. 1092-1096 in Vol. 2. In: Sybil P. Parker (editor-in-chief), *Synopsis and classification of living organisms*. McGraw Hill: New York. 2 vols. \$150.

Here is a significant work that should be at hand in every malacological laboratory. It is a detailed review down to the family and subfamily level of all living mollusks. Information about shell and anatomical morphology is presented, together with notes on distribution and a few key references. This is the first attempt to provide such a detailed overview since Thiele's *Handbuch der Systematischen Weichtierkunde* (1929-1935). It will provide both a handy reference for students of malacology and a stimulus to workers to fill in the significant gaps that exist in our knowledge of many molluscan groups.

Workers familiar with the literature on particular families will, of course, see that key points are missing and that there are misinterpretations. In a work of this magnitude, this is unavoidable, and its author is already soliciting comments for a proposed second, more-detailed edition, with far more illustrations (included to help define some of the terms used) than the few of this edition. One may hope that the Mollusca section by itself will be available separately by then so that specialists will not have to purchase the entire two-volume work.

It takes particular dedication and persistence to complete the important compilations that lay the groundwork for future contributions. Few have the stamina to attempt them and to avoid the distractions that the inadequacies in our knowledge and the contractions in the available literature present in virtually every group. Kenneth Boss deserves a great deal of credit for completing this task and for resolving to build on it as well.

Eugene Coan

Catalogue of the Living Bivalvia of the Eastern Pacific Ocean: Bering Strait to Cape Horn

by F. R. BERNARD. 1983. Canadian Special Publication of Fisheries and Aquatic Sciences 61, 102 pp. Price \$8.00 (Canadian) in Canada, \$9.60 elsewhere.

Students of any fauna are fortunate when there exists a checklist or catalogue listing all the described or recognized taxa in their special area—more so when data on geographic, geologic, and depth distribution are included. This work consists of a systematic catalogue and a bibliography of the primary descriptive literature on the living bivalves of a geographic swath 2000 km wide extending from the Bering Strait (66°N) to Cape Horn (60°S), along

with an impressive array of data concerning “where, when, and how deep.”

Like other works of equivalent scope, this one takes a few risks. Checklists do not readily admit multiple working hypotheses, and every taxonomist carries in his head numerous cases where the only proper systematic readout must be “wait and see.” Moreover, the coverage is vast—several geographic provinces and 1308 species. With the unprecedented number of biologists now concerned with bivalves and (at least peripherally) bivalve systematics, there are bound to be disagreements regarding form and content.

Each species entry includes a reference to the original description, and the same information for taxa regarded as synonyms. There are many nomenclatural innovations, mainly at the family, subfamily, and superfamily levels; an essay on the classification of Bivalvia gives the background on some of Bernard's taxonomic choices.

The geographic list continues the practice, originally proposed by SCHENCK & KEEN (1937) and implemented in KEEN's (1938) checklist, of giving the midpoint-of-range, the arithmetic mean of the north and south limits of distribution. Apparently a forthcoming paper by Bernard and another author will discuss the use of midpoint-of-range analysis. The method has found limited acceptance for the interpretation of paleoclimates. ALLISON's (1973) summary criticisms are perhaps the most cogent.

The depth ranges are said to include no depths based on dead and probably displaced material; this must have required some fine judgment as to which material was displaced and which was not.

A temperature range is given for each species, in “an attempt to supply another index useful for estimating paleotemperatures of Pleistocene bivalve faunas” (p. 2). Although it is stated that the computer-calculated value is the mean of the closest adjoining records, the statistic is nowhere defined. Are these mean annual temperatures? Mean maximum summer temperatures in the warm part of the range and mean minimum winter temperatures in the cold part? Historical maxima and minima? Or some other thermal measure? At depth, seasonal variation may not amount to much, but in shallow waters it can be considerable. For animals with seasonal cycles, the lowest (or highest) temperature at a particular time of year may be critical, the mean annual temperature hardly important. I cannot see using the Bernard figures as any sort of index without knowing for what they stand.

This part of the text speaks also of analysis using “the proportion of thermophilic and cryophilic species” (although it is not the *proportion* of thermophilics and cryophilics that indicates a minimal temperature range, as the text has it). Applied with caution, this is a useful type of

paleoclimatic analysis; it would have been helpful to cite examples and explanations of the technique, perhaps VALENTINE & MEADE (1961) or LINDBERG *et al.* (1980).

The geologic range information consists of the epoch name for the oldest known occurrence in the eastern Pacific. The standard is said to be the Pacific coast provincial megafossil chronology—as though there were one standard, or even one province, applicable from the Bering Sea to Cape Horn. No bibliographic reference is cited. The expression “Pacific coast provincial standard” has often been used to refer to the correlation chart of WEAVER *et al.* (1944), but the coverage of that work stops south of Alaska and north of the present-day tropical realm. The last 5–10 years have seen important revisions in the age assignments of tropical American Cenozoic sections. Most current biostratigraphy around the northeastern Pacific rim attempts to relate ages to the European series-epoch standard, and trans-Pacific correlations proceed on this basis as well. There is a strong current trend toward the use of regionally defined stages (*e.g.*, ADDICOTT, 1976) rather than epochs to classify the faunal succession in the provinces of the eastern Pacific. For these reasons, the epoch citations in the catalogue have limited utility.

Users need to double-check the epoch records anyway: *Glycymeris vancouverensis* Clark & Arnold, 1923, described from the Juanian Stage (earliest Miocene) Sooke Formation, appears under the synonymy of *G. corteziana* Dall, 1916, but only the age “Recent” is given.

It may come as a surprise that Bernard has chosen not to use the category of subspecies, even though “the majority of wide-ranging species are expected to yield several subspecies” (p. 1). As a heuristic device, this stance might be defensible. The criteria for recognizing a subspecies are, or ought to be, more restrictive than those for a species and the relevant tests have rarely been applied. Unfortunately, the treatment of taxa formerly regarded as subspecies is inconsistent and apparently subjective, some being synonymized and others showing up at the species rank.

A few typographic conventions are unfortunate. For instance, the centered geographic notes (“South Atlantic,” “Arctic Ocean”) stand out unnecessarily, while family, superfamily, and higher category names, at the left margin, recede into the background. Somewhat more serious are the numerous uncorrected typographic errors in the explanatory text—not because they themselves are confusing, but because they suggest that the catalogue itself may also fall short on accuracy. My response runs from the (probably pedantic) concern that some of the Latin names may not have been transcribed correctly (Is it *Rudiphaga* Olsson, 1961, or *Rupiphaga*?) to the fear that some of the depth or latitude citations may be flat-out erroneous because of typos.

Some overdue housecleaning disposes (by the best evidence possible) of the “questionables”—*e.g.*, *Pteria viridizona*—but it is also good that they remain in small type in the body of the list. The notes (pp. 67–70) are interesting for showing the many ways in which spurious rec-

ords can become entrenched in the literature. More “questionables” are bound to turn up; in other cases, it may be too early to write some of them off. For example, even if *Vulsella pacifica* (Dall, 1916) from Nicaragua is synonymous with the Indo-Pacific *V. mytilina* (Lamarck, 1819), might it not be another of the many cases of Indo-Pacific faunal elements present in the eastern Pacific, rather than malacologist error?

Not surprisingly, some familiar names get changed. In my opinion, demotion of *Hinnites* DeFrance, 1821, to a subgenus of *Chlamys* Röding, 1798, may not go far enough, because late cementation and opportunistic, irregular growth have evidently arisen independently many times. *Kellia lapereusii* (Deshayes, 1839) falls as a synonym of *K. suborbicularis* (Montagu, 1803), not unexpectedly, but one awaits the documentation.

The name *Panope abrupta* (Conrad, 1849) is used for the large, common bivalve of the northern Pacific usually known as *Panope* (or *Panopea*) *generosa* Gould, 1851. *Mya abrupta* Conrad, 1849, was rejected by early workers as a junior secondary homonym in the genus *Panopea*, and the junior name *P. generosa* used instead. MOORE (1963) restored the name *P. abrupta* on the grounds that *Pholadomya abrupta* Conrad, 1832, is not a *Panopea*, as it had been considered by previous workers. Under the current ICZN rules, however (“A junior secondary homonym rejected before 1961 is permanently rejected . . .”—Article 59[b][i]), the name *Panopea generosa* should stand. According to Bernard, the northwestern Pacific *Panopea japonica* (A. Adams, 1850) is indistinguishable from the American species; in this case, *P. japonica* is the earliest available name. Workers in the state of Washington, where this clam is something of a cultural hero, will undoubtedly be distressed.

I hope most users of Bernard’s catalogue will recognize that many of the assertions, synonymies, and taxonomic rankings are not yet rigorously demonstrated. The work is a better statement of the way things *might be* than we have had before. In its innovations, it calls upon thoughtful systematists to examine the evidence behind their own assumptions. That can be a disquieting experience, but as my systematics coach might say, “no pain, no gain!”

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Barry Roth

Fauna and Hydrobiology of the Shelf Zones of the Pacific Ocean

Proceedings of the XIV Pacific Science Congress (Khabarovsk, August 1979). Edited by O. G. Kussakin and A. I. Kafanov. Far East Science Center, Academy of Sciences of the USSR, Vladivostok, 148 pp. Price 1r 70k (about \$2.00 US) [in Russian with English summaries].

Of the 20 papers published in this volume from the marine biology section meeting, 9 treat mollusks or faunas that are predominantly molluscan. These papers cover a broad range of topics including ecology, paleontology, and biogeography.

A. J. Kohn combines paleontology with ecology and presents a preliminary report on the evolution of the Indo-

Pacific Conidae. Ecological work in the North Pacific includes investigations of *Mytilus edulis* communities in the Sea of Okhotsk by V. G. Averincev *et al.*, as well as a study of subtidal communities to a depth of 200 m along the east coast of Kamchatka by A. N. Golikov and O. A. Scarlato. From the South Pacific, E. W. Dawson presents distribution patterns for bathyal mollusks on the Campbell Plateau and Chatham Rise.

In the biogeographic realm, K. Y. Arakawa discusses the biogeography and ecology of sedentary invertebrates including three species of mollusks introduced into Japanese waters. On larger scales, K. N. Nesis examines the distribution of cephalopods in the Pacific Ocean and proposes zoogeographic provinces based on these distributions that are in turn compared to shelf provinces. J. C. Briggs establishes criteria for recognizing centers of origin and concludes that the central East Indies and the North Pacific Ocean have been important centers of origin for marine shelf faunas. Another dispersal view is presented by M. Horikoshi who examines larval transport, endemism, and reproductive mode of shelf and island faunas in the Pacific Ocean. A. I. Kafanov adds the indigenous species' competitive abilities to the dispersal model and examines the evolution of North Pacific molluscan faunas.

Because of the variety of topics, this proceedings volume and the individual papers that it contains will be of interest to many workers who study past and present North Pacific mollusks and their ways. Because the papers are written in Russian, let us hope that information regarding the existence of any English versions is forthcoming.

D. R. Lindberg

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Manuscripts must be typed on white paper, 8½" by 11", and double-spaced throughout (including references, figure legends, footnotes, and tables). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

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References in the text should be given by the name of the author(s) followed by the date of publication: for one author (SMITH, 1951), for two authors (SMITH & JONES, 1952), and for more than two (SMITH *et al.*, 1953).

The "literature cited" section must include all (but not additional) references quoted in the text. References should be listed in alphabetical order and typed on sheets separate from the text. Each citation must be complete and in the following form:

a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra*. *Veliger* 4:132-134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. *Living marine molluscs*. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117-135. *In*: R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal invertebrates of California*. Stanford Univ. Press: Stanford, Calif.

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Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend.

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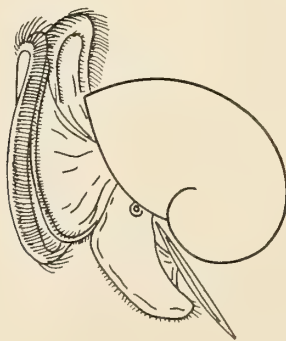
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